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A REVISION OF THE ALEPISAUROID FAMILY SCOPELARCHIDAE (PISCES: MYCTOPHIFORMES)

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ABSTRACT

The alepisauroid family Scopelarchidae contains 17 species arranged in four genera. Diagnostic characters for the recognition of species and genera include meristic and morphometric characters, osteological features, pigment patterns, larval morphology, and mode of larval development. All available characters are assembled to produce a proposed classification of the group based on inferred relationships between the various species. Analysis of the distribution of the 17 species reveals eight species limited to all or part of one water mass (including two species circumglobal in subantarctic and antarctic waters south of the Subtropical Convergence), seven species exhibiting distributions that cross water mass boundaries and show varying degrees of warm-water cosmopolitanism (although no species is cosmopolitan), and two species too poorly known for their distributions to be characterized. A comparison between inferred relationships of the various species and their geographical distribution suggests that evolution in the family has resulted in two main lineages, one radiating into low productivity central portions of the central gyrals, the other radiating into northern and southern subpolar and polar waters.

INTRODUCTION

The alepisauroid family Scopelarchidae, the pearl-eyed fishes, is a widespread, but, until now, very poorly known group of large-bodied, midwater predators. Most of the problems in the taxonomy of scopelarchids have stemmed from a lack of material, resulting in inadequate descriptions of species or in descriptions based on larval material. Twenty-four nominal species of scopelarchids have been described and seven nominal genera established to contain them. I recognize 17 species and four genera.

The listing of nominal species and genera below summarizes the taxonomic conclusions of this study. Names are listed in chronological order of their appearance in the literature, with the original combination on the left and the currently recognized combination (if different from the original) on the right.

Scopelarchus Alcock 1896

Type species: Scopelarchus guentheri Alcock 1896	
Scopelarchus guentheri Alcock 1896	
Dissomma anale Brauer 1902	= S. analis (Brauer)
Odontostomus perarmatus Roule 1916	= S. analis (Brauer)
Scopelarchus michaelsarsi Koefoed 1955	
Scopelarchus cavei Marshall 1955	= S. michaelsarsi Koefoed
Scopelarchus beebei Rofen 1963	= S. analis (Brauer)
Scopelarchus candelops Rofen 1963	= S. analis (Brauer)
Scopelarchus sagax Rofen 1963	= S. analis (Brauer)
Scopelarchus stephensi Johnson 1974	

Dissomma Brauer 1902 = Scopelarchus Alcock 1896

Type species: Dissomma anale Brauer 1902

Benthalbella Zugmayer 1911a

Type species: Benthalbella infans Zugmayer 1911a Benthalbella infans Zugmayer 1911a Scopelarchus elongatus Norman 1937

= B. elongata (Norman)

= S. analis (Brauer)

Neoscopelarchoides dentatus Chapman 1939 Scopelarchus linguidens Mead and Böhlke 1953

Benthalbella diaphana Rass 1955

Neoscopelarchoides dubius Marshall 1955 Benthalbella macropinna Bussing and Bussing 1966

Scopelarchoides Parr 1929

= B. dentata (Chapman)

- = B. linguidens
- (Mead and Böhlke) = *B. linguidens*
- (Mead and Böhlke)
- = B. infans Zugmayer

Type species: Scopelarchoides nicholsi Parr 1929 Scopelarchoides nicholsi Parr 1929 Scopelarchoides kreffti Johnson 1972 Scopelarchoides climax Johnson 1974 Scopelarchoides danae Johnson 1974 Scopelarchoides signifer Johnson 1974

Neoscopelarchoides Chapman 1939 = *Benthalbella* Zugmayer 1911a

Type species: Neoscopelarchoides dentatus Chapman 1939 = B. dentata (Chapman)

Phanops Rofen 1963 = Scopelarchus Alcock 1896

Type species: Phanops michaelsarsi (Koefoed) 1955

= S. michaelsarsi Koefoed

Rosenblattichthys Johnson 1974

Type species: *Phanops volucris* Rofen 1966 *Phanops volucris* Rofen 1966 *Benthalbella alata* Fourmanoir 1971 *Rosenblattichthys hubbsi* Johnson 1974 = *R. volucris* (Rofen) = *R. volucris* (Rofen)

= R. alatus (Fourmanoir)

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METHODS

DESCRIPTIONS

In the descriptions of the various taxa of scopelarchids, I have attempted to prevent redundancy by including characters common to all members of a taxon only in the description of that taxon. Where present, the bracketed line on all figures indicates 1.00 mm.

MATERIAL EXAMINED

The following abbreviations are used in reference to material examined:

CAS: California Academy of Sciences, San Francisco.

- DANA: Carlsbergfondets DANA-Ekspeditioner, Marinbiologisk Laboratorium Charlottenlund Slot, Denmark; DANA further abbreviated to letter D in listing of material examined. All DANA material now deposited at Zoological Museum, University of Copenhagen.
- ISH: Institut für Seefischerei, Bundesforschungsanstalt für Fischerei, Hamburg, Germany; material listed either by ISH catalogue number or WALTHER HERWIG (WH) station number.
- FMNH: Field Museum of Natural History, Chicago, Illinois. Material listed by catalogue number.
- LACM: Los Angeles County Museum of Natural History, Los Angeles, California; LACM-E, material deposited at LACM listed by USNS ELTANIN station numbers; LACM-V, material deposited at LACM listed by R/V VELERO IV station numbers.
- NMFS: National Marine Fisheries Service, Honolulu, Hawaii; material listed by ship and station number: HMS, R/V HUGH M. SMITH; JRM, R/V JOHN R. MANNING.
- ORSTOM: Office de la Recherche Scientifique et Technique Outre-Mer, Noumea, New Caledonia; material listed by name of ship, cruise, and station number, or by date of capture.
- OSU: Oregon State University, Corvallis, Oregon.
- SIO: Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California.

- SOSC: Smithsonian Oceanographic Sorting Center, Smithsonian Institution, Washington, D. C. Material listed by ship, cruise, and station number: AB, R/V ANTON BRUUN; E, USNS ELTANIN; TV, R/V TE VEGA. All SOSC material deposited at National Museum of Natural History.
- UH: Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii; material listed by date of capture: year/month/collection number.
- USC: University of Southern California, Los Angeles, California; material listed by USNS Eltanin (USC-E) or R/V Velero IV (USC-V) station numbers.
- USNM: National Museum of Natural History, Smithsonian Institution, Washington, D. C. Material listed as follows: 1. USNM catalogue number; 2. ACRE, Ocean Acre Expeditions, material listed by cruise and station number; 3. uncatalogued material listed by ship, cruise, and station number: AB, R/V ANTON BRUUN; E, USNS ELTANIN; TV, R/V TE VEGA.
- WHOI: Woods Hole Oceanographic Institution, Woods Hole, Massachusetts. Material listed by Richard H. Backus (RHB) station numbers.

The listing of material examined includes only the institutional catalogue or station numbers, the number of specimens, and the size range (in mm.) represented. Complete locality and capture data may be obtained from the respective institutions or from the author. Most of the specimens were taken in one of the following types of nets: Isaacs-Kidd Midwater Trawl (IKMT), CMBT 1600 midwater trawl employed on *FFS "Walther Herwig"*, 1 m. plankton net (MN), 2 m. stramin net (2mSN), or the conical nets used by the R/S Dana (S150, S200, E300 etc.)

Counts and Measurements

Unless specified below, methods for taking counts and measurements follow those given by Hubbs and Lagler (1958). The last rays of the dorsal and anal fins are divided completely to the base, and in each case were counted as one. All vertebral centra were counted, including the compound element supporting the parhypural and hypurals. Counts of vertebrae were made from radiographs and from cleared and stained material.

All measurements are straight-line point-to-point measurements, taken to the nearest 0.1 mm. with dial calipers or needle-point dividers, or to the nearest 0.01 mm. with an ocular micrometer. All measurements smaller than 5.0 mm. were made with an ocular micrometer.

- Adipose fin: distance to midcaudal rays = distance between end of adipose base and base of upper midcaudal ray. Length of base = greatest overall basal length, but excluding any fleshy ridge extending anterior to fin. Length of fin = distance between angle of posterior margin of adipose fin with body to tip of fin.
- Anus to anal origin = distance between midpoint of vent and base of first anal ray.
- Dorsal fin: dorsal origin to anal origin = distance between verticals through bases of first fin rays of each fin. End of dorsal base to base of midcaudal rays = distance between base of last dorsal ray and base of upper midcaudal ray.
- Pectoral insertion to pelvic insertion = pectoral-pelvic distance = distance between upper margin of base of dorsalmost ray of each fin.
- Pelvic insertion to anal origin = pelvic-anal distance = distance between uppermost portion of base of dorsalmost pelvic ray and base of first anal ray.

Snout to anus = distance from tip of snout to midpoint of vent.

Snout to anal fin, pectoral fin, pelvic fin = in each case distance from tip of snout to base of first (or dorsalmost) ray of each fin.

All fish lengths given are standard lengths (S.L.). All measurements were taken on specimens preserved in 5 or 10 per cent formalin, 40 per cent isopropanol, or 70 per cent ethanol, most having originally been preserved in formalin. No attempt was made to determine error due to shrinkage.

OSTEOLOGY

Osteology was studied from trypsin-prepared cleared and stained material following the method of Taylor (1967). The procedure used in studying the prepared material closely follows that of Paxton (1972). Nomenclature of the bones is discussed under each osteological section.

LATERAL LINE SCALES

Counts of lateral line scales were of all countable elements (either the scales or scale pockets), including the ultimate, invariably imperforate, scale. Lateral line scales in scopelarchids consist of a large bony plate pierced by a moderate to large central pore, and a bony shelf, the tympanum, attached posterior to the pore and partly or wholly covering the pore (fig. 2). Lateral line scales were removed for measurement from four positions along the lateral line:

lateral line scale above pectoral insertion = any of four to five scales above pectoral base.

- lateral line scale above anal origin = any of four scales anterior or posterior to vertical through base of first anal ray.
- penultimate lateral line scale = next to most posterior scale in lateral line series.
- ultimate lateral line scale = posteriormost scale in lateral line series, this scale, unlike all that precede it, is invariably imperforate in scopelarchids, and invariably lacks a tympanum.

Measurements of the proportions of lateral line scales were made to 0.01 mm. with an ocular micrometer and included the following:

length = greatest anterior to posterior longitudinal distance.

height = greatest depth of scale (dorsal - ventral dimension).

tympanum height = greatest dorsal-ventral depth of tympanum.

pore height = greatest dorsal-ventral depth of pore.

The following ratios compared transverse measurements with the length of the lateral line scale:

H/L = height divided by length.

T/L = tympanum height divided by length.

P/L = pore height divided by length.

SYSTEMATICS

Order MYCTOPHIFORMES

The Myctophiformes (Iniomi) form an apparently natural group of 16 families classified variously as a suborder (Greenwood et al., 1966, p. 395), a full order (Gosline et al., 1966, pp. 1-5), or as an order solely constituting a superorder (Rosen and Patterson, 1969, p. 460). The following definition of the Myctophiformes is based on Regan (1911), Harry (1952), Gosline et. al. (1966), and my own work (Rosen has recently (1973, Suppl. No. 1 to Zool. Jour. Linnean Soc., pp. 397-513) removed the families Myctophidae and Neoscopelidae from other iniomous fishes to form a much restricted Order Myctophiformes. The remaining iniom families are placed in a new order, Aulopiformes. This article was received too late to be more than mentioned in the present work.).

Marine fishes with pelvics abdominal in position; gas bladder present or absent; pelvic bones free from cleithra; adipose dorsal fin typically present; maxillary bones excluded from gape by premaxillaries; no mesocoracoid; typically a process from palatine bone, supported by a lateral projection from the ethmoid, the palatine process directed upward and outward and overlapping proximal end of maxillary; no ethmoidal commissure, this replaced by a typically complete cross-connection between supraorbital canals just behind the orbits; gill openings wide; pectoral girdle typically attached to skull by forked posttemporal; vertebral centra co-ossified with arches; fusion of innermost pterygiophore of pelvic fin with innermost pelvic ray; ovaries with oviducts.

No single one of these characters will separate all myctophiform from all salmoniform fishes; a number of exceptions are pointed out by Gosline et. al (1966) while other exceptions (particularly the connection of the palatine with the maxillary, and the shape of the posttem poral bone) are pointed out for scopelarchids later in this paper. Nevertheless, most recent authors feel the assemblage to be a natural one, and while no single diagnostic characters exists for the group, no salmoniform fish is known to exhibit all of the characters exhibited by myctophiforms.

The group is an old one with a fossil record extending back to the Upper Cretaceous (e.g., Goody, 1969). However, because of the frag-

mentary nature of the fossil record, the time of origin of many recent groups is unknown. Paralepidids are known from the Miocene (e.g., Harry, 1953) but there are no known fossil scopelarchids.

The 16 families of myctophiform fishes are divided into two suborders: (1) Myctophoidei, an assemblage of 10 families, including species ranging in habitats from estuarine and near shore neritic to the deep sea benthos. Three myctophoid families, Myctophidae, Neoscopelidae, and Scopelosauridae, occur in oceanic midwaters, and the Myctophidae with more than 30 genera and over 200 species is by far the most diverse family of oceanic inioms. (2) Alepisauroidei, a group of six families, exclusively oceanic and meso or bathypelagic in habitat. The following definition of the suborder is based on Regan (1911), Harry (1952), Gosline et al. (1966), and my own work.

Suborder Alepisauroidei

Large oceanic midwater predators lacking a gas bladder; lower jaw teeth, if present, in 2-3 series, outermost fixed, innermost depressible; upper jaw teeth uniserial, generally small, numerous (more than 20), fixed; palatine teeth in 1-2 rows; normal gill rakers absent, replaced in most by gill teeth fixed on bony plates; body scales absent in all but scopelarchids and paralepidine paralepidids; 3-4 + 4-5 branchiostegal rays; intramuscular bones present in all 6 families; pelvics abdominal with strong tendency to have 9 pelvic rays; independently ossified parietals present or absent; all are probably synchronous hermaphrodites with functional ovotestis; luminescent organs present in at least some paralepidids and scopelarchids.

Although no single one of these characters is diagnostic, most authors are convinced that this suborder forms a natural group. The earliest known alepisauroid is from the Eocene, but authors knowledgeable of the fossil record of myctophiform fishes have stated that the group probably had its origin in the Upper Cretaceous and certainly by the beginning of the Tertiary (Harry, 1952; Goody, 1969).

A number of trends exhibited by alepisauroid myctophiformes have been discussed by Marshall (1955) and Gosline et. al. (1966).

1. Ossification of bones in most alepisauroids is light, no doubt related to the problem of maintaining position in the water column (these fishes lack gas bladders). It has been suggested by Gosline et al. (1966 p. 10) that the form and fin pattern of alepisauroids suggests a hovering and darting, pike-like way of hunting. This has been borne out, at least partially, by the discovery that at least some paralepidids orient and hover vertically in the water column (Houot, 1958; Peres, 1958). 2. No doubt the loss of body scales by all alepisauroids other than scopelarchids and paralepidine paralepidids is related to decreasing the overall density of the fish, but may in part be related to the ability of many alepisauroids to engorge large masses of food at one time. *Alepisaurus, Omosudis, Anotopterus,* and *Evermannella* are all able to engorge relatively large prey, and juvenile paralepidids have been caught with vastly expanded stomachs. Scopelarchids, however, are not known to have this ability, despite their truly formidable dentition.

3. The pectoral fins are generally low on the body in Alepisauroids and the angle of insertion of the pectoral with the body tends to be less than 45°. Marshall (1955) suggested that the low, flat setting of the pectorals allowed them to act as paravanes providing lift during swimming. In myctophoids the pectorals tend to be inserted well up on the side of the body, at an angle greater than 45° with the body, and are probably used in braking and maneuvering.

4. All six families of Alepisauroidei are synchronous hermaphrodites, possessing a functional ovitestis (Gibbs, pers. comm.). Alepisauroids are large, relatively "rare," high-trophic-level midwater predators. In an environment where food is probably limiting, one would expect that for the larger predators, availability of mates might become an important factor in the ecology of populations. If this is true, then it is possible to envision the clear-cut advantage to an individual to be able to mate with any other individual (or perhaps even self-fertilize). A clear-cut advantage to the population is also present in that synchronous hermaphroditism results in the population having a 100 per cent female-biomass-to-population-biomass ratio.

The most recent revision of the various alepisauroid families other than the scopelarchids are as follows: Alepisauridae, Gibbs and Wilimovsky (1966); Anotopteridae, Rofen (1966c); Evermannellidae, Rofen (1966d); Omosudidae, Rofen (1966b); Paralepididae, Rofen (1966a). A key distinguishing the various families of myctophiforms from one another as well as from "isospondylous" fishes is presented by Bigelow (1963, pp. 97-104), but must be used with some degree of caution.

Family Scopelarchidae

Type-genus.—Scopelarchus Alcock 1896.

Diagnosis.—Alepisauroids with basihyal moderately short to elongate, but well-ossified; lingual teeth strong, straight to strongly hooked, present over basihyal, present or absent over basibranchials; body and postorbital regions of head completely covered with cycloid scales; parietal bones, when present, small, widely separated by frontals and supraoccipital; eyes large, tubular directed straight upward except in three species where directed dorsoanteriad; coracoid broadly expanded; two postcleithra, widely separated in vertical dimension; larvae with 0-3 peritoneal sections.

Description.-Dorsal 5-10, Anal 17-39, Pectoral 18-28, Pelvic 9, Caudal 1 + 9 + 8 + 1 (counting from dorsal), Branchiostegal rays 4 + 4. Vertebrae 40 to 65. Short to moderately elongate with shallow to deep body. Jaws neither prolonged nor massive, but large relative to head length, upper jaw extending beyond vertical through middle of eye. Moderately to strongly compressed. Nostrils situated far forward of eye, anteriorly on each side of snout. Three pores situated over nasal bone medial to each pair of nostrils, anterior and posterior pores larger than the middle pore. Two sclerotic bones in anterior and posterior wall of evestalk. Lateral line papillae generally present in two patches on snout, one patch medial to each nasal bone. Three vertical series of sensory papillae on snout, one posterior, one ventral, and one immediately anterior to nostrils. Scales covering body and postorbital regions of head cycloid, lacking radii, circuli incomplete on most body scales with only an anterior field present. Lateral line scales large, consisting of a large bony plate pierced by a moderate to large pore, and with a bony shelf, the tympanum, attached only behind (posterior to) the pore, typanum completely covering pore or covering all but anterior portion of pore. Fins soft-raved. Dorsal small with relatively short rays. Dorsal origin well before midlength of body. Anal base short to elongate, distinctly longer than head. Anal origin at (one species) or well behind midlength. Caudal forked, the adjacent procurrent rays well developed. Pelvics abdominal, inserted from in advance of dorsal origin to distinctly behind dorsal base. Pectoral fin inserted at about one-third of body depth from ventral contour of body at a slight to moderately steep angle with body, but angle of insertion not exceeding 45°. Dorsal adipose fin well-developed, inserted over posterior one-third of anal base (except on one species where inserted entirely behind anal base). Anus slightly in advance of anal origin.

Interorbital region extremely narrow, interorbital width less to considerably less than eye diameter. An iridescent white oval of connective tissue on side of eye tube, termed the "pearl organ." Lower jaw slightly to distinctly arched, arching upward distally and projecting slightly beyond upper jaw. Premaxillary teeth small, uniserial, retrorse over most of premaxillary length but straight posteriorly, fixed. Dentary teeth in two rows, the outer teeth small and fixed, the medial teeth large lance olate canines. Palatine teeth in one or two irregular rows, more medial and anterior teeth are large lanceolate canines. Vomerine teeth small, one per side (with rare exception). Lingual teeth uniserial, larger in size





anteriorly but more strongly hooked posteriorly, present over basihyal or over basihyal and first two or three basibranchials. Supramaxillary present or absent. Antorbital present or absent. Supraorbital present or absent. Gills 4. Gill rakers reduced to small gill teeth arranged on bony plates. Three supraneurals. Intramuscular bones present. Synchronous hermaphrodites with functional ovotestes. At least one species (*Benthalbella infans*) known to be luminescent.

Remarks.—Scopelarchids are distinguished among other alepisauroids by the possession of strongly developed, usually hooked, lingual teeth, and by the large tubular eyes, directed straight upward or slightly dorsoanteriad. Scopelarchids constitute a group of 17 species arranged in four genera. All four genera occur in all three oceans (fig. 1). Characters considered to be diagnostic at the generic and specific level are indicated in the next several pages, followed by an account of what little is known about the habits and ecology of scopelarchids.

Diagnostic characters.—

MERISTIC CHARACTERS: Meristic characters utilized to distinguish species of scopelarchids include counts of the following: dorsal fin, anal fin, pectoral fin, lateral line scales, and vertebrae. Branchiostegal rays are invariably 8, and pelvic rays (despite Rofen, 1966e, p. 568) are invariably 9.

Tables 1-5 compare meristic characters for all 17 species of scopelarchids. For most species the range in counts is 2-3 dorsal rays, 4-5 anal rays, 5-6 lateral line scales, and 4-6 vertebrae. In almost all cases strong modality of the central 2-3 values of the range is evident. Of 120 possible (Rosenblattichthys hubbsi is known only from the holotype and is excluded) comparisons between species (N(N-1)/2), 111 species pairs can be uniquely separated, without overlap in ranges, by a combination of two or more of the following counts: dorsal, anal, pectoral, lateral line scales (note, however, the dearth of specimens of Benthalbella linguidens. Rosenblattichthys alatus, Scopelarchoides climax, and S. kreffti). If we allow an overlap in range of one value (but only where modal values are distinctly different), this increases to 114/120 possible comparisons. Of these, 35 pairs are separable on the basis of only one character whereas 81 are separable on the basis of two or more characters. The species pairs which cannot be separated in this fashion (but may differ statistically in meristic counts) are the following: Scopelarchus analis cf. S. guentheri, Scopelarchoides danae, and S. nicholsi; Rosenblattichthys alatus cf. R. volucris; Scopelarchus michaelsarsi cf. S. stephensi; and Scopelarchus guentheri cf. Scopelarchoides danae. These latter species can easily be separated from one another by other characters. Thus meristic characters

A. Dorsal fin rays	5	6	7	8	9	10	N
B. macropinna	10	18	_	_	_	_	28
B. dentata	—	12	25	5	_	—	42
S. nicholsi	—	6	116	_	_	—	122
S. danae	—	1	11	46	3	_	61
S. climax	_	—	1	7	_	_	8
S. analis	_	_	18	197	11	_	226
S. guentheri	—	_	38	62	—	_	100
S. michaelsarsi	—	—	2	23	1	_	26
B. infans	_	—	—	1	49	—	50
B. linguidens	—	_	—	1	8	—	9
R. alatus	—	—	—	3	8	_	11
R. hubbsi	_	_	_	1	_	_	1
S. stephensi	—	—	_	16	—	—	16
B. elongata	_	_	_	_	23	4	27
R. volucris	_	_	_	_	30	1	31
S. signifer			_	_	42	1	43
S. kreffti	_	—	_		9	—	9

TABLE 1. Comparison of meristic characters in scopelarchids.

alone are sufficient to diagnose most of the species. It can also be seen that *Benthalbella* has the most vertebrae (54 to 65) and lateral line scales (54-66), *Scopelarchus* the least (40-51 and 40-52), with *Rosenblattichthys* (46-51 and 47-53) and *Scopelarchoides* (45-56 and 46-59) intermediate.

MORPHOMETRIC CHARACTERS: In all, 31 measurements of various body proportions were taken from a representative sample over the available size range for each species. In all cases the ranges for these 31 proportions overlapped, usually significantly or completely in comparisons between genera. In certain cases morphometric characters were useful in distinguishing between pairs of species (see *S. michaelsarsi* and *S. stephensi*) but in all cases more easily obtainable characters are available, and I have not included tables comparing morphometric characters between species at this point. All measurements are based on post-metamorphic specimens. Proportions of the various body measurements taken were found to be remarkably non-allometric (with the exception of body depth which increases and interorbital width which decreases with length) in the species analyzed for allometry (especially those of *Scopelarchus*). Thus in the descriptions of species only the range and mean of the various proportions are given.

LATERAL LINE SCALES: The shape of the lateral line scales, the depth and shape of the tympanum, the size of the central pore, and the degree to which the tympanum covers the pore, are distinctive, in combin-

	TABLE	z. Con	ipariso	1 10 UC	neristi	c char	acters	In sco	pelarc	spin:					
B. Anal fin rays	17	18	19	20	21	22	23	24	25	26	27	28	29	30	Z
B. dentata	5	6	10	∞	1	I	I	I	I	L	I	I	I	I	29
S. michaelsarsi	I	2	11	00	10	I	I	I	I	I	I	I		I	36
B. infans	I	I	I	2	13	6	2	00	00	I	I	I	I	I	50
S. nicholsi	I	I	I	က	60	56	4	I	I	I	I	1		I	123
S. stephensi	I	I	I	6	10	က	I	I	I	I			I	1	22
R. alatus	1	I	I	1	ß	6	63	1	I	I	1	I	I	I	18
R. volucris	I	I	I	I	0	00	22	00	I	I	1	I	I	I	40
S. analis	Ι	I	I	I	4	39	53	97	39	S	1	I	I	I	237
R. hubbsi	I	I	I	I	I	I	I	1	I	I	I	I	I	I	==1
B. elongata	I	I	I	I	I	I	I	က	00	19	6	1	I	I	40
S. danae	I	I	I	I	I	I	I	0	25	31	4	1	I	I	62
S. guentheri	I	1	I	I	I	I	I	က	25	39	25	13	0	I	107
S. climax	I	I	I	I	1	I	I	1	1	S	1	I	I	I	2
S. kreffti	Ι	I	I	1	I	I	I	Ι	1	2	9	I	I	I	6
S. signifer	I	I	I	I	I	1	I	I	I	2	18	14	0	I	36
B. linguidens	I		I	I	I	I	I	I	I	I	I	2	က	1	6
B. Anal fin rays	31	32	33	34	35	36	37	38	39	40					z
B. macropinna	l		I		4	12	7	4	1	I					28

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C. Pectoral fin rays	18	19	20	21	22	23	24	25	26	27	28	z
S. guentheri	34	62	6	2	I		I		I	I	I	107
S. analis	10	54	120	52	1	I	I	I	I	Ι	Ι	237
S. michaelsarsi	5	11	14	9	I	I	I	I	I	Ι	I	36
S. stephensi	9	12	4	I	I	I	I	I	I	I	I	22
B. elongata	Ι	1	15	16	7	-1	I	I	I	I	I	40
S. danae	Ι	I	19	32	11	I	I	I	I	I	I	62
S. nicholsi	I	I	5	65	50	က	I	I	I	I		123
R. hubbsi	I	Ι	I	1	Ι	I	Ι	Ι	I		I	1
B. dentata	I	Ι	I	1	4	10	14	Ι	I	I	I	29
R. alatus	I	Ι	I	Ι	က	4	-	5	5		I	18
S. signifer	I		I	I	5	20	10	1	I	I	I	36
R. volucris	I	I	I	I	I	2	11	19	80	I	1	40
S. kreffti	I	I	I	I	I	7	7	1	I	1	I	6
B. linguidens	Ι	I	I	Ι	I	I	က	9	I	I	I	6
B. infans	I	Ι	I	Ι	Ι	I	I	7	23	15	က	48
B. macropinna	I	Ι	I	Ι	Ι	I	Ι	10	15	က	 	28
S. climax	I	I	I	Ι	Ι	I	Ι	4	Ι		I	4

			,												
D. Lateral line scales	40	41	42	43	44	45	46	47	48	49	50	51	52	53	Z
S. michaelsarsi	7	Ω.	n	1	4	I	I	I	I	I		I	I		20
S. stephensi	I	က	1	5	4	I	I		I	I	I		I		13
S. analis	I	I			I	က	24	33	54	32	2	I	I		148
S. nicholsi	Ι		I			I	61	11	26	00	1				48
S. guentheri	I	I	I		I			9	12	20	18	15	1		72
R. alatus	I	I	I	I	I	I	I	1	0		I	I	I		က
R. volucris	I	I	I	I		I			1	0	0	1	I		9
S. signifer	I	I	I	I	ļ	I	I		I	က	10	9	1	I	20
S. danae	I	I	I	I	I	I		I	I	I	9	21	10	I	37
R. hubbsi	I	I	I	I	I	I	I		I	I	I	I	I	1	1
S. climax	I	I	I	I	I	I	I	I	I	I		I	I	1	1
D. Lateral line scales	54	55	56	57	58	59	60	61	62	63	64	65	66	67	Z
B. dentata	7	10	က	6	1	I	I	I	I	I	I		I	I	18
B. infans	I	2		4	1	1									00
S. kreffti	I				1	1		I			I			I	2
B. elongata	I	I	I	I	I	I	I	က	4	00	4	5	I		24
B. macropinna	I	I	I	I	I	I			က	9	9	0		I	17
B. linguidens	I	I					I						1		1

TABLE 4. Comparison of meristic characters in scopelarchids.

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ation, for all known species of scopelarchids (fig. 2). Particularly useful is the lateral line scale above the anal origin because the combination of its characteristics is unique, as far as known, for each species and in my material, scales in this region are most often retained when other lateral line scales have been lost due to damage during capture.

OSTEOLOGICAL CHARACTERS: Characters obtained from osteological studies have been most useful in delimitation of genera. A subsequent section is devoted to osteological studies.

FIN PLACEMENT AND LENGTH: Scopelarchids differ in placement of the pelvic fins (pelvic insertion before, under, or behind dorsal base), relative lengths of the pectoral and pelvic fins; origin of the anal fin (at or well behind midlength); insertion of the dorsal adipose fin (adipose base entirely before or entirely after vertical through last anal ray); and distance from the adipose fin to the base of the midcaudal rays.

PIGMENTATION: I have divided the pigmentation of scopelarchids into three categories: accessory pigment spots or areas (see larval characters below), dermal pigmentation, and epidermal pigmentation. Dermal pigmentation refers to the major pigment stripes present in some genera and species (fig. 54). These develop prior to metamorphosis, and persist in the adult. In most cases this pigment comes to be partially or completely overlain by the epidermal pigmentation associated primarily with the scale pockets. This usage is more or less consistent with that of Bertelsen (1951, p. 12) who distinguished between skin and subdermal pigmentation in ceratioid larvae. No histological determination has been made, and my terminology is mainly based on the usefulness between distinguishing major pigment areas acquired before metamorphosis, and the more or less general and more superficial pigmentation acquired during and after metamorphosis. Species possessing dermal pigmentation in this sense are as follows: Scopelarchus, all four species have pigment stripes dorsal and ventral to the lateral line scales from the rear of the caudal peduncle to moderately in advance of the anal origin; Scopelarchoides, dermal pigmentation present as distinctive pigment stripes concentrated ventral (S. danae, S. nicholsi) or dorsal (S. kreffti) to lateral line or absent (S. signifer, S. climax); Rosenblattichthys, scattered large melanophores appearing middorsally and spreading to cover most of body dorsal to lateral line, with an additional dense band of pigmentation present ventral to lateral line in larger specimens of R. volucris. Dermal pigmentation is absent in Benthalbella.

Other differences in pigmentation are mainly useful in diagnosing species or distinguishing between related species, e.g., a cap of enlarged black melanophores covering the dorsal margin of the pearl organ is known only in *Benthalbella macropinna* and *Scopelarchoides climax; Scopel*-



FIG. 2. Lateral line scale above anal origin in scopelarchids. Relationships between species as in Figure 60 (lengths of line segments are arbitrary). A. Rosenblattichthys volucris, LACM 9806, 103.5. B. R. hubbsi, ISH 2219/71, 144.5. C. Scopelarchoides nicholsi, S1065-243, 104.1 D. S. danae, DANA 3828 VII, 121.2. E. Scopelarchus guentheri, USNM Scopelarchoides signifer, ORSTOM 21/2/69, 83.0. J. S. climax, SIO 70-107, 99.3. K. S. kreffri, ISH 1561, 159.0. L. [35417, 93.6. F. S. analis, UH 69/11/1, 52.8. G. S. michaelsarsi, ISH 783, 96.8. H. S. stephensi, SIO68-483, 60.5. I. Benthalbella macropinna, LACM 10135, 178,6 M. B. dentata, S1067-104, 151.8. N. B. infans, DANA 3624 1, 132.1. 0. B. linguidens, OSU 568, 221.0. P. B. elongata, USC-E 1036, 200.0.

All measurements (standard length) follow specimen numbers and are given in millimeters.

archoides danae, S. nicholsi, and S. signifer differ in development of pigment on dorsal and ventral lobes of caudal fin, concentrated on dorsal lobe (S. signifer), ventral lobe (S. danae) or equally well-developed on both lobes (S. signifer); Scopelarchus guentheri differs from all other species of Scopelarchus in lacking pigment on or at the base of the pectoral fin.

LUMINESCENCE: Luminescent tissue is at present known to occur only in *Benthalbella infans* and its presence in *Scopelarchoides kreffti* is highly probable (see below).

LARVAL CHARACTERISTICS: Larval morphology is extremely useful in defining genera. The following characters of larvae are especially useful:

- 1. Form. Larvae of scopelarchids range from extremely elongate and shallow (*Benthalbella*) to short and deep (*Rosenblattichthys* and some species of *Scopelarchoides* and *Scopelarchus*).
- 2. *Size.* Larvae of *Benthalbella* achieve exceedingly large size (50-100 mm.) while retaining larval morphology. Larvae of other species metamorphose or acquire most adult characters at a size considerably less than this.
- 3. Metamorphosis. Larvae of Benthalbella undergo rapid metamorphosis after a prolonged period of growth while retaining larval form, and acquire adult characters over a very small increment of size. Larvae of other scopelarchid genera acquire adult characters essentially one by one, undergoing gradual metamorphosis over a size range usually from 15-40 or 50 mm.
- 4. Fins. The pectoral fins of Rosenblattichthys are precocious, developing ossified rays well in advance of the median (except the caudal) or pelvic fins. In other scopelarchids all other fins have completely differentiated rays before the ventral portion of the pectoral fin possesses ossified rays. In Scopelarchoides and Rosenblattichthys the pelvic fins appear as buds on the midlateral abdominal cavity wall, well above the level of the intestine. In Benthalbella and Scopelarchus the pelvic fin buds appear ventrolaterally at or beneath the level of the intestine (which occurs midventrally in the abdominal cavity in all four genera). In Benthalbella, except B. macropinna, the pelvic fin insertion in larvae is well in advance of the dorsal origin: in all other scopelarchid larvae the pelvic fin insertion is beneath or well behind the dorsal base.
- 5. *Pigmentation*. Accessory pigment spots or areas in scopelarchids are defined as prominent pigment spots or areas apparent in the smallest (6-12 mm.) available larvae of any species in which they oc-

cur. Accessory pigment spots are remarkably constant and their pattern is unique for each species known to possess them. In Rosenblattichthys the middorsal and ventral pigment spots and areas are entirely in advance of the rear of the adipose base and the last anal ray respectively. In Scopelarchoides the middorsal spot, if present, and the midventral spot (except for that associated with the anus in S. nicholsi and S. danae) are entirely behind the adipose base and last anal ray respectively. Accessory pigment spots or areas are present in Rosenblattichthys (fig. 29) and Scopelarchoides (fig. 37) (larvae of S. kreffti unknown) and are absent in Scopelarchus and Benthalbella. Other differences in larval pigmentation include differences in origin and pattern of dermal pigment (see above), peritoneal pigment (see below), and differences diagnostic for a given species or species pair (e.g., presence of melanophores on pectoral fin in Benthalbella dentata and B. macropinna before the pectoral rays are ossified but not after).

- 6. *Meristic characters.* Counts of fin rays do not differ between larval and adult specimens.
- 7. Peritoneal pigment. In all adult scopelarchids except Benthalbella elongata, the gut is completely enclosed by a uniform tube of brown to jet-black (in alcohol) peritoneal pigment. This pigment appears in larvae, however, in a fashion characteristic for each genus or group of apparently related species. Benthalbella lacks peritoneal pigment in larvae prior to metamorphosis. Associated with the appearance of peritoneal pigment are a rapid elongation of the gut, rearward expansion of the caecum (see below), investiture of the abdominal cavity wall with musculature (except B. macropinna where this is delayed), appearance of gonad, appearance of scales, particularly lateral line scales, and first appearance of head and body pigmentation. All of these changes occur over a short increment of growth (see fig. 18). In all other scopelarchids peritoneal pigment is present before most or any of these latter, adult characters have been acquired, and often before the ossification of fin rays has occurred. In larvae possessing peritoneal pigment it occurs in one or three sections. These sections consist of well-defined, prominent sheets of pigmented tissue within the abdominal cavity, and are separated over a long interval of growth after first appearance in species in which more than one section appears. One section only is found in Rosenblattichthys, Scopelarchoides signifer, and S. climax. Three sections, a single anterior and two paired posterior, are found in Scopelarchoides nicholsi and S. danae, as well as in all four species of Scopelarchus. However, in S. danae and S. nicholsi the posterior

sections appear significantly later (based only on the increment in size) than the anterior section and appear above (*S. danae*) or well in advance of pelvic base (*S. nicholsi*). In *Scopelarchus* larvae the peritoneal sections all appear with near synchrony (based only on size) and the posterior sections appear well to the rear of the pelvic base. In all cases the peritoneal sections expand and fuse together by the end of metamorphosis producing the uniform tube of pigment around the gut characteristic of adults.

Aspects of the biology of scopelarchids.—

SAMPLING DIFFICULTIES: Scopelarchids, particularly adults, are relatively rare in collections. In a series of 1600 tows to all depths and generally of 4-5 hours duration, the Bermuda Oceanographic Expeditions of the New York Zoological Society apparently captured only 20 scopelarchids, and only two of these were adults [Rofen (1966e) records 23 specimens, but three are probably not scopelarchids (see S. analis)]. On the Antipodes Expedition (SIO 1970) using a 10 ft. IKMT and fishing in a stepped-trawl with a slow-oblique tow-between-steps hauling plan (28 tows, each tow of 5-10 hours duration), only 18 scopelarchids were taken, one adult and 17 larvae and juveniles. These 18 specimens, however, included all seven species known to occur in the area of the Antipodes transect (Philippine and South China Seas). These results appear to be typical not only for scopelarchids but for the other alepisauroid families as well. Adults are not known for a large number of paralepidid species. Previous authors have attributed much of this to sampling difficulties. Alepisauroids are thought to be excellent examples of net avoiders, being large and thought to be capable of swift movement, at least over a short period of time (Gibbs and Wilimovsky, 1966; Rofen, 1966a-e). The problems of avoidance have been considered by a number of authors (among them Binns (1959), Barkley (1964), McGowan and Fraundorf (1966), Brinton (1967), Harrison (1967), and Clutter and Anraku (1968)). As scopelarchids are rarely taken, and very rarely are more than one or two individuals taken in a haul, and as virtually all have been taken in open, non-closing gear of a variety of kinds (the 11 scopelarchids known to have been caught in closing-gear are listed in Norman, 1937, p. 86; Nybelin, 1948, pp. 40-44; Marshall, 1955, pp. 309-310; and Harrisson, 1967, p. 78; and are listed under the appropriate species: Benthalbella elongata, B. infans, and Scopelarchus analis), I have not attempted the various subtractive methods of a number of previous authors (among them Bertelsen, 1951; Gibbs, 1969; Roper, 1969). It is also rather difficult to imagine a technique for placing any kind of confidence limits on the assumptions of "productive layers" that some of these methods require. The majority of adult scopelarchids in my material came from hauls to between 500-1000 m., although there is a good indication that the adults of a number of species (e.g., *Scopelarchoides nicholsi*) occur, at least at night, a good deal shoaler than this. Larvae of most species are known from hauls within the upper 100-200 m., and several species are represented by larvae that have been taken in hauls within the top 30-40 m. A vast majority of hauls successfully capturing scopelarchids have been at night, but the data are too poor to allow any statement concerning the possibility of diurnal vertical migration in scopelarchids. To my knowledge scopelarchids, unlike paralepidids, have never been taken at the surface at night.

SIZE AND HABITS: Scopelarchids reach a relatively large size for midwater fishes. The largest-bodied species are those of the genus *Benthalbella* and *Scopelarchoides kreffti*. Size records for the family include: *Benthalbella elongata*, 234.0 mm.; *Benthalbella macropinna*, 233.5 mm.; *B. linguidens*, 221.0 mm.; *B. dentata*, 203.0 mm.; *Scopelarchoides kreffti*, 187.5 mm.; *Rosenblattichthys hubbsi*, 144.5 mm.; *Benthalbella infans*, 137.4 mm. The remaining species in the family are not known from specimens larger than 100-125 mm.

No systematic analysis of the gut contents of scopelarchids was attempted, since most specimens examined had no recognizable contents, but I have found fishes in varying degrees of digestion in a number of the species. The identifiable gut contents included *Cyclothone* and *Vinciguerria* (both gonostomatids) and several species of myctophids. Fishes known to prey on scopelarchids include *Alepisaurus ferox* (Maul, 1946, p. 20) and *Aphanopus carbo* (Trichiuridae) (Rofen, 1966e, p. 569). Fitch and Brownell (1968, p. 2568) record an otolith of "*Benthalbella* sp." from a spinner porpoise (*Stenella longirostris*) netted between 12 and 20° N in the eastern tropical Pacific. This is an intriguing record as the only species of scopelarchid known to occur in the eastern tropical Pacific between 12 and 20° N is *Scopelarchoides nicholsi*.

Scopelarchids have a tremendously well-developed caecum (= stomach?) extending as a muscular blind pouch to near the anus in the adults of most species. The only food items discovered within scopelarchids have been from the caecum, not from the thin-walled slender intestine. Perhaps the function of this caecum is in storage, and may be an adaptation for extraction of all possible nourishment from ingested food particles. Scopelarchids are apparently not capable of engorgement of large particles of food at one time as are omosudids (in one case an 18 mm. fish was extracted from an *Omosudis* only 7 mm. long and another specimen of *Omosudis* was found to have eaten a squid as large as itself, 6.6 mm. (Rofen, 1966b, p. 477)), alepisaurids, anotopterids, evermannel-

lids, and at least some paralepidids (Gibbs and Wilimovsky, 1966; Rofen, 1966a-e). Food items known to be taken by other alepisauroids include squid, octopods, tunicates, crustaceans, and fishes, including each other. Predators on other alepisauroids include tunas, whales, marlin, and pelagic sharks. All alepisauroids are thought to be "pike-like" in habit, hovering and darting, capable of swift movement over short intervals of time, but not sustaining continuous high-speed motion. This supposition, partly borne out by bathyscaphe observations of paralepidids (Houot, 1958; Peres, 1958), is based mainly on the reduction in musculature and skeletal ossification exhibited by a number of these fishes (Marshall, 1955; Gosline et al., 1966). However, scopelarchids possess scales, and do not present the classic alepisauroid picture of reduced ossification and musculature. Based on radiographs and upon observation, the bones in scopelarchids appear to be well-ossified, and the muscle masses appear to be well-developed. How well the scopelarchids fit the picture painted by Gosline et al. (1966) remains to be tested.

REPRODUCTION: Details of gonadal structure and development will be described in a later publication but all scopelarchid species thus far examined (from all four genera) have been found to be synchronous hermaphrodites with a functional ovotestis quite similar to that described for other alepisauroids and other inioms (Mead, 1960; Gosline et al., 1966; Nielsen, 1966).

LUMINESCENCE: Scopelarchids were not known to be luminescent until the recent discovery of ventral bioluminescent organs in *Benthalbella infans* reported by Merrett et al. (1971). The following description of luminescent organs in this species is abstracted from their paper.

Photogenic tissue first appears in larval *B. infans* as pearl-white paired ellipsoidal blocks of tissue visible through the transparent ventral abdominal body wall, and much resembling the developing musculature of the pelvic fin. This musculature of the pelvic fin is itself suspected to be photogenic. Sectioning revealed two separate blocks of this tissue, each block consisting of paired sections arranged symmetrically around the ventral midline, one just posterior to the pelvic fin base, termed the POp, the other just anterior to the anus, termed the AO. The musculature of the pelvic fin, suspected of bioluminescence, is termed the POa organ.

Confirmation of the presence of bioluminescence in *B. infans* was obtained with the capture of an adult specimen. Upon stimulation with hydrogen peroxide it was observed to produce light of a blue-green color from three discrete midventral regions, corresponding to the POp and AO, but not the POa. Instead, light appeared in the muscle mass of the isthmus and this organ was termed the 10 organ. The ratio of light intensities IO:POp:AO was 1:7:5.5. All three light producing areas are diffuse
sources of light with minimal directional capabilities.

The IO organ produced light of low intensity, and lacked the layer of translucent tissue ventral to the other organs and also lacked any reflector layer or pigment background. Sections were made of the POa, POp, and ΔO organs and histological studies revealed the cells of the photogenic tissue to be arranged in blocks, with cell boundaries ill-defined, and with nuclei lying along the periphery of each block. The authors point out a similarity of this arrangement to muscle tissue, and hypothethize that the photogenic tissue of *B. infans* is modified muscle tissue, making the photogenic organs of *B. infans* unique. The photogenic tissue lies internal to masses of muscle tissue through which the light must pass, and which may act as light-diffusing organs. The arrangement of the photogenic tissue is said to be histologically similar to that of the adjacent external muscle tissue, and the authors report a zone of cell blocks of intermediate staining and cytological properties between the photogenic tissue and muscle, offering further confirmation that the luminous tissue may be modified muscle. A multilayered reflector with a pigment lining lies internal to the photogenic tissue.

In my material the POp and AO are evident as paired small masses of tissue, yellow or white in color, much resembling muscle tissue, readily visible in most adult specimens, lying behind the pelvic fin base and immediately anterior to the anus, with a line of dark pigment between them running along the ventral midline. The authors have confirmed the presence of the AO and POp in the type of *B. dubius* (Marshall) and suggest the probable identity of this species with *B. infans* Zugmayer. A suggestion with which I fully concur. The authors also examined specimens of *B. elongata* and *B. macropinna*, and could find no such structures. I have re-examined numerous specimens of *B. dentata*, *B. elongata*, *B. macropinna*, and the only known adult of *B. linguidens*, and I can find no such structures in any of these species.

However, Scopelarchoides kreffti, the only other scopelarchid with a very dark longitudinal stripe of pigment at the ventral midline, undoubtedly has an AO organ. An organ that very closely resembles the AO organ described by Merrett et al. (1971) just anterior to the anus is present in *S. kreffti* and visible in my material of *B. infans.* No sign of a POp organ was seen in *S. kreffti*.

The only other alepisauroid inioms known to possess luminescent organs are paralepidids of the genera *Lestidium* and *Lestrolepis*. In *Lestidium* the luminous organ, located in the midventral musculature, is a single, discreet, self-luminous duct, not connected externally and extending from the isthmus to the pelvic fins (Rofen, 1966a). However, Graae (1967) described *Lestidium bigelowi* as a paralepidid with discrete photophores located in the midventral line, one each on the isthmus, between the pectoral fins, and just posterior to the pelvic fin bases. Histological examination revealed these to be rather typical discrete photophores with pigment lining and a lens. In other characters, *Lestidium bigelowi* was found to be intermediate between *Lestidiops* (which lacks luminous tissue, as far as known) and *Lestidium*, and was referred to *Lestidium* because of the presence of luminous tissue. The other genus of luminous paralepidids is *Lestrolepis*, possessing luminous ducts similar in position to those of *Lestidium*, but paired over most of their length, connected anteriorly and posteriorly, and not connected to the outside. In both *Lestidium* and *Lestidiops* the light produced is said to be a steady yellow glow (Rofen, 1966a, p. 371).

VISION: One of the more remarkable characteristics of scopelarchids is their possession of tubular eyes directed straight upward or dorsoanteriad (three species). A patch of iridescent white tissue, generally ellipsoidal to oval in outline, is present on the side of the eyestalk. This organ, termed the pearl-organ, lending the family its common name of pearleved fishes, was thought by some authors to be luminous, but is probably instead simply glistening white connective tissue. Brauer (1908) termed the pearl organ the "lens pad" and thought it to be involved in the retraction of the lens into the eve-tube. Munk (1966) has discounted this idea. suggesting instead the pearl organ may be a modified argentea. Argentea are guanine-bearing layers of tissue that increase the opacity of the iris in larval fishes (Walls, 1942, p. 236). Its function in the scopelarchid eve is obscure, but layers of shining tissue similar to it, if not so strongly developed, can be seen in the eyes of at least some evermannellids and in Ichthyococcus (Gonostomatidae), both tubular eyed fishes. Munk (1966) reviews the literature on tubular eved fishes and reports on the structure of a large number of them. In his literature review Munk discounts some of the suggestions concerning the function of tubular eyes, e.g., Wall's (1942) suggestion that the division of the retina into main (located ventrally) and accessory (located on the medial wall of the eve-tube) suggests that tubular-eved fishes are bifocal, perceiving distant objects on the accessory retina and near objects on the main retina. He further discounts, on physical grounds, that the large lens of tubular-eyed fishes increases the intensity of the image on the retina. Munk (1966, p. 48) concludes that tubular-eyes are modified to produce an enlarged (but not brighter) image on the main retina, the accessory retina is not optically adjusted, and that the binocular visual field is enlarged owing to the parallel main axes of the eye, possibly increasing sensitivity to light and a better judgment of distances. The enlargement of the image on the main retina, increasing the resolving power of the main retina, is at the expense

of optical adjustment (i.e., image-formation) of the accessory retina. The retina of scopelarchids is a pure rod retina, with normal teleost rods, as an adaptation to poor lighting conditions.

The limit of man's ability to detect light is a light intensity about 10^{-12} that of sunlight at noon, about the same as that of an epipelagic fish (Clutter and Anraku, 1968). It has been suggested (Brett, 1957; Denton and Warren, 1957) that the eyes of midwater fishes may be 10-100 times more sensitive than this. Harrisson (1967) reported light in the Canary Basin to be 10^{-8} that of surface intensity at 520 m., or well within the range of fish receptive abilities. Moreover, work by Clarke and Denton (1963) suggested that fishes dwelling in the Sargasso Sea should be able to detect surface light to depths as great as 1100 m. All of these estimates are within or below the probable depth range of most scopelarchid species, and no doubt the eyes of scopelarchids are an adaptation for feeding, either by perception of silhouettes or perhaps the ventral bioluminescence of their prey.

OSTEOLOGY

Only three papers have dealt with osteological characters of the Scopelarchidae. Parr (1929) studied the osteology of only two species, and Rofen (1966e) and Rosen and Patterson (1969) considered a limited number of characters. My studies of the osteology of scopelarchids are based on 11 of the 17 species (six species had to be partly excluded due to lack of material) and all four genera.

A definitive terminology for all the various elements of the teleosteon skeleton is not available because of doubt and controversy over the homologies of a number of bones. The terminology I have adopted is consistent with most of the recent ichthyological literature. As different sources of terminology were used for different portions of the skeleton, I have indicated the sources used for each section at the beginning of the section.

Listing of cleared and stained material.— Scopelarchidae Benthalbella B. dentata

			 	 	 	 	 	SI	070-19,	1 (203.0)
B .	elongata .		 	 	 	 	 	.USC-	E 1392,	1 (126.1)
В.	infans		 	 	 	 	 	UH '	70/9/15	, 1 (95.6)
В.	macropinn	ia .	 	 	 	 	 	.USC-	E 1671,	1 (113.5)
Rose	nblattichth	vs								
<i>R</i> .	volucris		 	 	 	 	 	LACM	1 9806,	1 (103.5)

..... S1063-379, 1 (118.0)

S. danae
S. nicholsi S1065-243, 1 (103.2)
S. signiferORSTOM, CYCLONE V - 2, 1 (104.6)
Scopelarchus
S. analisUH 70 9/12, 1 (95.0)
S. guentheri
S. michaelsarsi
Alepisauridae
Alepisaurus sp
Anotopteridae
Anotopterus pharao
Aulopidae
Aulopus japonicus
Chlorophthalmidae
Chlorophthalnus agassizi
Parasudis truculentus FMNH 67156, 1 (87.5
Evermannellidae
Coccorella atrata
Evermannella indica FMNH 49876, 1 (73.5)
Odontostomops normalops S1068-447, 1 (78.7)
Neoscopelidae
Neoscopelus microchir FMNH 66741, 1 (77.0)
Notosudidae
Scopelosaurus sp
Omosudidae
Omosudis Iowei
Paralepididae
Macroparalepis sp FMNH 49988, 1 (190.0)
Notolepis sp
Paralepis sp
Synodontidae
Saurida brasiliensis FMNH 64810, 1 (84.0)
Synodus intermedius FMNH 66029, 1 (107.5)
Trachinocephalus my ops FMNH 45392, 1 (81.1)

Cranium.-

In scopelarchids the ethmoid cartilage and 15 bones, 10 paired and five median, constitute the cranium (figs. 3, 4). These bones include the following: basioccipital (BOC), dermethmoid (DEM), epiotics (EPO), exoccipitals (EXO), frontals (FR), lateral ethmoids (LEM), opisthotics (OPO = intercalars), parietals (P), parasphenoid (PAS), prootics (PRO), pterosphenoids (PTS), pterotics (PTO), supraoccipital (SOC), sphenotics (SPO), and vomer (V). My terminology for these elements follows that of Weitzman (1967).



FIG. 3. Cranium of Scopelarchidae. A. Ventral view of cranium of *Benthalbella dentata*, S1070-19, 203.0. Left palatine bone left in place. B. Dorsal view of posterior portion of cranium in *Scopelarchus guentheri*, S1069-21, 112-4 Frontals detached. Line of attachment of frontals over supraoccipital shown by broken double line. C. Dorsal view of cranium of *Scopelarchoides signifer*. ORSTOM CYCLONE V-2, 104.6. Nasal bones left in place.

ETHMOID REGION: Ethmoid region consisting of central mass of ethmoid cartilage, paired lateral ethmoids, and dermethmoid. Ethmoid cartilage single, covered dorsally by dermethmoid over anterior onethird of its length, covered over posterior two-thirds of length by frontals. Ethmoid cartilage separating dermethmoid from vomer and parasphenoid. Dermethmoid forming thin canopy over ethmoid cartilage, and in turn overlain posteriorly by anterior end of frontals. A strong ligament connecting proximal head of premaxillary with dermethmoid. Lateral ethmoids prominent, sheath-like bones enclosing lateral projections of ethmoid cartilage anteriorly, dorsally, and posteriorly. Cartilaginous core of lateral ethmoid forming a major point of abutment of palatine and a strong ligament connects palatine to lateral ethmoid bone.

VOMER: Vomer a moderately elongate, triangular, sheath-like bone. Head of vomer lying ventral to ethmoid cartilage, and bearing ventrally one or two small teeth per side. A fossa on each side of vomer contributing to support of head of palatine bone of that side. Posteriorly tapering shaft of vomer rests in an elongate shallow fossa in anterior portion of parasphenoid.

FRONTALS: Frontals the largest, most complex bones of dorsal skull roof, meeting tightly but not fusing in midlongitudinal line. Anteriorly frontals overlie posterior portion of dermethmoid, as well as a posterodorsad directed process of ethmoid cartilage.

The extremely narrow interorbital of most scopelarchids results from each frontal forming a tube, opening anteriorly on a flattened terminal plate, and posteriorly through pores just behind the interorbital region. A thin septum, presumably composed of medial walls of each frontal tube, separates the two frontals in midlongitudinal line of interorbital region in most species. In *B. dentata* and *B. elongata* there is no median septum, rather the frontal tubes of each side are divided by a deep groove in midlongitudinal line. The interorbital tubes are incomplete dorsally in my material of Scopelarchoides nicholsi, S. danae, Scopelarchus michaelsarsi, and S. stephensi. This may reflect incomplete development in the two Scopelarchoides species but probably reflects the adult condition in the two species of Scopelarchus, whose wide flaring frontals and consequently wide interorbital region, result from incomplete formation of frontal tubes. This would appear to be a retention of a larval character in these latter two species, for in all species of Scopelarchus, the interorbital roof is non-ossified in larvae.

Pores in interorbital area marking passage of supraorbital laterosensory canal connecting nasal, pterotic, and infraorbital canals. Supraorbital canal enclosed by frontals in interorbital region and posteriorly continuing laterad on each side within a trough-like portion of the frontals, passing laterally from the frontals to the dermosphenotic (sixth infraorbital). Length of trough-like portion of frontals exceeding that of dermosphenotic in all species except *B. dentata*, where the expanded troughlike dermosphenotics extend medially almost to the interorbital area, at dorsoposterior corner of orbit.

Posteriorly frontals forming a thin sheet of bone overlying anterior

portions of supraoccipital and epiotics, and articulating with or overlain by parietals (where present), and forming part of narrow roof over posttemporal fossae. Frontals articulating laterally with pterotics and sphenotics and anteriorly with pterosphenoids. Frontals greatly expanded posteriorly in *Scopelarchus*, occupying one-half or more of postorbital dorsal skull roof. Frontals restricted to anterior one-third of postorbital dorsal skull roof in all other genera (fig. 3).

PARIETALS: Although most definitions of the Scopelarchidae (Parr, 1929; Marshall, 1955; Gosline et al., 1966; but not Rofen, 1966e) have stated that the parietals are indistinguishably fused with the frontals, this is not true for most scopelarchid species (fig. 3). Parietals thin, small, plate-like bones overlying frontals, supraoccipital, and epiotics at common border of these bones in *Scopelarchoides signifer* and *Benthalbella*. Parietals present in *Rosenblattichthys volucris*, but much reduced in size. In no case are parietals large and they are always widely separated.

Parietals apparently absent in *Scopelarchoides danae*, *S. nicholsi*, and all species of *Scopelarchus*. The loss of parietals, especially in *Scopelarchus*, is no doubt related to rearward expansion of the frontals. As Parr (1929) based his osteological definition of the family on *Scopelarchoides nicholsi* and *Scopelarchus analis*, his statement that scopelarchids lack parietals was correct for the material with which he dealt.

SUPRAOCCIPITAL: In Scopelarchoides, Rosenblattichthys, and Benthalbella, supraoccipital a large oblong bone occupying much of postorbital dorsal skull roof. In Scopelarchus the frontals are expanded posteriorly, and the supraoccipital occupies less than half of the postorbital dorsal skull roof, but contributes greatly to the posterior wall of the cranium. Supraoccipital spine in Scopelarchus located at or below posterior dorsal margin of cranium. This condition is partially true of Scopelarchoides nicholsi and S. danae where the supraoccipital spine is shifted to the posterior of the dorsal roof of the cranium.

A spike-like elongate supraoccipital spine present in *Scopelarchoides* signifer and *Benthalbella*. In *Scopelarchoides nicholsi, S. danae,* and *Scopelarchus* spine present as the short, blunt knob of bone at anterior end of low ridge of bone, a supraoccipital crest, limited to posterior one-third of supraoccipital. In *Rosenblattichthys* a distinctive supraoccipital crest, a low ridge of bone, extending entire length of supraoccipital, dividing left from right frontals in midline where these latter bones overlie anterior portion of supraoccipital.

EPIOTICS: In most scopelarchids epiotics are large flat bones forming a considerable portion of the lateral postorbital skull roof. Epiotics overlain by frontals and parietals anteriorly, contacting supraoccipital medially, the pterotics laterally within the posttemporal fossae, and the exoccipitals posteriorly. Large rugose knob at center of each epiotic attached via a ligament to part of anterior body musculature. Another ligament attaching epiotics to dorsal limb of posttemporal. Concomitant with rearward expansion of frontals in *Scopelarchus*, epiotics shifted somewhat posteriad, contributing significantly to posterior wall of cranium.

EXOCCIPITALS: Exoccipitals most posterior bones of cranium, approaching each other closely above foramen magnum, and articulating dorsally and anteriorly with epiotics and supraoccipital, ventrally with basioccipital, dorsally with pterotics and opisthotics, and anteroventrally with prootics. Joint between exoccipitals and supraoccipital interrupted by wide area of cartilage. Posteriorly and dorsally exoccipitals partly covered by neural arch of first vertebra and connected to it by extremely strong fibrous ligamentous tissue.

OPISTHOTICS (= INTERCALARS): Opisthotics sit astride posterolateral joint between exoccipitals and pterotics. A ligament extending from a bony knob on opisthotic of each side connecting it to posttemporal of that side. In *Rosenblattichthys, Scopelarchoides,* and *Scopelarchus* an anteroventral prong from opisthotic reaches or almost reaches border of prootic. An anteroventrally directed prong on opisthotic apparently absent in *Benthalbella*.

BASIOCCIPITAL: Basioccipital forming posterior portion of cranial floor. Basioccipital meeting parasphenoid and prootics anteriorly and exoccipitals dorsally. A strong, fibrous, ligamentous tissue connection between centrum-like posterior face of basioccipital and first vertebral centrum.

PTEROTICS: Pterotics forming posterolateral corner of skull roof, articulating anteriorly with sphenotics, posteriorly and ventrally with exoccipitals and opisthotics, and ventrally with prootics. Pterotics meeting epiotics laterally in posttemporal fossae. Dorsal troughlike surface of pterotics carrying temporal canal from dermosphenotic (sixth infraorbital) to second extrascapular. Posteroventrally located fossa in pterotic receiving posterior head of hyomandibular. Narrow roof over anterior portion of posttemporal fossa formed of a thin shelf of bone provided mainly by pterotic and abutting on epiotic.

SPHENOTICS (AUTOSPHENOTICS): Sphenotics forming lateral margin of posterodorsal orbit, meeting prootics ventrally, pterotics posteriorly, frontals and pterosphenoids medially. No prominent sphenotic spine. Sphenotics overlain dorsally by dermosphenotics (sixth infraorbitals).

PROOTICS: Prootics extensive, contributing in large measure to posterior wall of orbit, and ventral and lateral walls of cranial vault.



FIG. 4. Cranium of scopelarchids. A. Lateral view of cranium of *Benthalbella dentata*, S1070-19, 203.0. B-C. Opisthotics of scopelarchids: B. Lateral view of left opisthotic, *B dentata*, S1070-19, 203.0; C. Medial view of right opisthotic, *Scopelarchoides signifer*, ORSTOM CYCLONE V-2, 104.6; D. Medial view of right opisthotic of *Scopelarchus guentheri*, S1069-21, 112.4.

Each prootic contacts its fellow of the opposite side dorsal to the welldeveloped myodome. Each prootic penetrated by a number of foramina. Prootics meeting parasphenoid ventrally, basioccipital posteriorly, and pterosphenoid, sphenotics, and pterotics dorsally.

PTEROSPHENOIDS: Pterosphenoids forming major portion of posterior wall of orbit dorsal to the prootics, meeting the frontals dorsally and sphenotics dorsolaterally. There is no orbitosphenoid or basisphenoid.

PARASPHENOID: Parasphenoid elongate, forming much of ventral contour of cranium. Anteriorly parasphenoid lying between ethmoid cartilage and vomer. Posteriorly two dorsolateral wings of parasphenoid meet with prootics while parasphenoid articulates medially with the basioccipital.

OTOLITHS: Apparently all scopelarchids possess all three pairs of otoliths. Sagittae large and quite evident in *Scopelarchoides* and *Scopelarchus*, and apparently smaller in *Benthalbella*. Due to a lack of fresh material, no detailed studies of otoliths were made. The otolith of *Scopelarchus analis* is pictured in Kotthaus (1967).

Superficial dermal bones.—

This section discusses the superficial dermal bones of the snout and orbital regions. Included are the following bones: antorbital (AO), infraorbitals (IO, IO1-6), nasals (NA), and supraorbital (SO). My terminology for these elements follows that of Smith and Bailey (1962), Gardiner (1963), and Weitzmann (1967).

NASALS: Nasal bones paired, small, thin, troughlike bones, one on each side of snout above dermethmoid. Nasals immediately anterior to anterior margin of frontals from which they receive the supraorbital laterosensory canal.

ANTORBITALS: Antorbitals, when present; splintlike to oblong bones attached on either side to a projection or stiffened ridge at anterodorsal margin of first infraorbital. Antorbitals in scopelarchids associated neither with laterosensory system nor with nasal bones, unlike myctophids in which antorbitals are in close association with or attached to the nasals (Paxton, 1972). Antorbitals are present in *Scopelarchoides, Rosenblattichthys*, and *Benthalbella macropinna*. Antorbitals absent in *Scopelarchus* and remaining species of *Benthalbella*.

SUPRAORBITALS: A separate bony element, tear-drop shaped, with blunt end dorsad, is present dorsal to antorbital in *Rosenblattichthys* volucris and *R. hubbsi* (fig. 5). From its position relative to the antorbital and frontal, and in comparison with other alepisauroids (e.g., *Paralepis*), I conclude that this element is a supraorbital. If so, *R. volucris* and *R.*



FIG. 5. Bones of infraorbital series of Scopelarchidae. A. Scopelarchoides signifer, ORSTOM CYCLONE V-2, 104.6. B. Benthalbella elongata, USC-E 1392, 126.1. C. Rosenblattichthys volucris, LACM 9806, 103.5. D. Scopelarchus analis, UH 70/9/12, 95.0.

hubbsi are the only known scopelarchids and to my knowledge the only alepisauroids to possess both antorbitals and supraorbitals. I have not yet confirmed the presence of this bone in *R. alatus.*

INFRAORBITAL (CIRCUMORBITAL) SERIES: Scopelarchids possess six infraorbitals numbered from anterior to posterior, all carrying in turn a segment of infraorbital laterosensory canal. Although a rounded concave surface on dorsomedial sides of infraorbitals 1, 2, and in some 3, would appear to contribute to the support of the eye, there is no distinct subocular shelf as reported from various acanthopterygians by Smith and Bailey (1962) and from myctophids by Paxton (1972).

INFRAORBITAL 1 (IO1 = lachrymal): IO1 elongate oblong plate with raised shelf of bone along dorsolateral margin (fig. 5). Pores in both plate and shelf, irregularly arranged. IO1 largest infraorbital bone in most scopelarchids. A distinct ethmoid process, overlying and connected with the lateral ethmoid, present in *Scopelarchoides signifer, S. nicholsi, S.* danae, and Scopelarchus. Ethmoid process absent in Benthalbella and Rosenblattichthys, as well as Scopelarchoides climax and S. kreffti.

INFRAORBITALS 2 AND 3 (102, 103). IO2 and IO3 most variable of all infraorbital bones in scopelarchids. In Scopelarchoides signifer IO2 an elongate curving bony plate supporting a wide elongate dorsolateral shelf. Plate of IO2 overlain laterally by IO1 but shelf of IO2 overlying surface of IO1, forming a strong brace between the two elements. IO3 in S. signifer basically Y-shaped, elongate in vertical rather than horizontal dimension, leg of "Y" lying dorsally and trough-shaped. Anterior fork of "Y" medial to IO2 while posterior fork forms posteroventral angle of infraorbital series, both forks consisting of plates of bone. IO2 and IO3 essentially identical in conformation to S. signifer in S. climax, S. kreffti, and Benthalbella macropinna.

IO2 and IO3 in *Rosenblattichthys* spp. somewhat similar in conformation to those of *S. signifer*, but in *Rosenblattichthys* the IO2 is considerably deeper and not so long, while the IO3 is quite deep but not Y-shaped. IO2 nearly excluding IO3 from posteroventral angle of infraorbital series.

In Scopelarchoides nicholsi, S. danae, and Scopelarchus, there is a trend in reduction of the size of the IO3 and a great increase in the relative size of the IO2. In S. nicholsi and S. danae IO3 reduced to a plate-like bone underlying posterodorsal corner of IO2, completely excluded from posteroventral corner of infraorbital series. In Scopelarchus IO2 provided with a posteroventrally-directed prong extending far posterior to a vertical through posterior margin of any other infraorbital bone, and forming posteroventral angle of infraorbital series (fig. 5).

In Benthalbella elongata, B. infans, and B. linguidens, position of IO2 and IO3 similar to S. nicholsi and S. danae, but whereas IO2 in S. nicholsi and S. danae is shortened in longitudinal dimension and triangular in shape, IO2 of the three Benthalbella species similar in dimensions and shape to that of S. signifer, S. climax, S. kreffti, and B. macropinna. IO2 in B. dentata greatly expanded, but lacking a dorsolateral shelf, a unique feature of this species.

INFRAORBITALS 4 AND 5 (104, 105). IO4 and IO5 similar in all scopelarchids, relatively small, trough-shaped bones pierced by a single pore. An anterior projection from 105 over posterior margin of eye occurs in *Scopelarchus*, and is especially evident in *S. analis* and *S. michaelsarsi*.

INFRAORBITAL 6 (106 = dermosphenotic). IO6 a thin, platelike bone overlying sphenotic and bordered by frontal, pterotic, and IO5. An anterior ridge of bone on IO6 paralleling anterior margin of sphenotic and forming a semi-canal passing laterosensory canal from frontal to



FIG. 6. Mandibular arch in scopelarchids. A. Upper jaw, lateral view, *Scopelarchoides* signifer, S1068-534, 70.0. B. Lower jaw, medial view, *Rosenblattichthys volucris*, LACM 9806, 103.5.

105. 106 enlarged, reaching to posteromedial dorsal corner of orbit in *Benthalbella dentata*.

Mandibular arch.—

The mandibular arch consists of the upper and lower jaws. The paired elements of the mandibular arch include the following bones: premaxillaries (PMX), maxillaries (MX), supramaxillaries (SMX), dentaries (D), articulars (AR), angulars (AN), Meckel's cartilages (MC), and coronomeckelian bones (sesamoid articulars) (CMN). This terminology follows that of Weitzmann (1967), Tominaga (1968), and Paxton (1972).

UPPER JAW—PREMAXILLARIES. Each premaxillary a sheathlike, relatively deep, dentigerous bone, tapering posteriorly. Premaxillary largely overlain laterally by maxillary and connected by connective tissue to it. Immediately anterior to maxillary fossa for palatine, premaxillary emerges from beneath maxillary and articulates with a projection from proximal head of maxillary (fig. 6). Dorsal and medial to premaxillary-maxillary articulation, premaxillary has a rounded ascending process converging with its fellow of the opposite side in midline. There is no premaxillarypalatine ligament such as that reported for neoscopelids by Greenwood et al. (1966). Jaws large in all scopelarchid species. Premaxillary teeth small, uniserial, retrorse anteriorly but straight posteriorly. A tendency in large adult scopelarchids to lose anterior premaxillary teeth, apparently without replacement.

UPPER JAW — MAXILLARIES. Each maxillary sheathlike and relatively deep over most of its length. Anteriorly a maxillary fossa receives cartilaginous articulatory process from palatine (fig. 6). Proximal head of maxillary exhibiting two projections anterior to maxillary-palatine articulation: one directed anteriorly, the other medially. Anterior projection supporting ascending process of premaxillary ventrally. Medial projection converging with its fellow of the opposite side in midline. A heavy ligament connects middle of proximal head of maxillary with lateral rostral margin of dermethmoid.

UPPER JAW—SUPRAMAXILLARIES: One supramaxillary present in most scopelarchid species. Supramaxillary large, one-third to one-fourth maxillary length, in *Scopelarchoides signifer*, *S. climax*, *S. kreffti*, *Benthalbella macropinna*, *Rosenblattichthys volucris*, and *R. hubbsi*. Supramaxillary shorter in *S. nicholsi* and *S. danae*, and splintlike in *Scopelarchus guentheri* and remaining species of *Benthalbella*. Supramaxillaries absent in *Scopelarchus analis*, *S. michaelsarsi*, and *S. stephensi*. Parr (1929, p. 12) reported the absence of supramaxillaries in *S. analis*.

LOWER JAW—DENTARIES: Dentaries the largest and most complex bones of the lower jaw. Dentaries consisting of a dorsal dentigerous ridge, a midlateral ridge, and a ventral sheet of bone. Teeth of lower jaw in two series: a lateral series of small, conical, slightly recurved teeth, numbering 30 or more in adults, and often hidden beneath a sheath of skin; an inner row of 15 or fewer lanceolate canines, the anterior 5-6 being large fangs. A row of partially ossified replacement teeth occurring medially to inner row of fangs. Preoperculomandibular cephalic sensory canal completely encased in bone on anterior of each dentary and partly so posteriorly. Medial face of dentary with elongate concave groove receiving anterior end of dorsal portion of articular and anteroventrally supporting anterior portion of elongate Meckel's cartilage. Dentary ending anteriorly in a projection, meeting and connected strongly to its fellow from the opposite side in midline.

LOWER JAW—ARTICULARS: Articulars forming posterior one-half of lower jaws, each articular divided into dorsal and ventral portions by the elongate bar of Meckel's cartilage (fig. 6). A dorsoposterior projection of lower portion of articular, the retroarticular process, supporting articulation of quadrate and receiving preoperculomandibular cephalic sensory canal from preopercle. Sensory canal completely enclosed in bone in ventral portion of articular. Dorsal to articulation of the quadrate, a dorsal articular process is connected by ligaments to distal end of maxillary and posterior end of dentary. Anterior portions of articular lying medial to and overlain anteriorly by dentary.

LOWER JAW—ANGULARS: Each angular a small irregularly shaped bone on medial surface of articular and at posteroventral corner of lower jaw. Angular connected by ligaments to interopercle.

LOWER JAW—CORONOMECKELIAN BONES: Each coronomeckelian is a small nodule of bone lying lateral to Meckel's cartilage and just anterior to anterior border of retroarticular region of articular. A strong ligament connecting coronomeckelian with pars mandibularis of adductor mandibularis muscle (Weitzmann, 1967; Paxton, 1972).

Palatine arch.-

The palatine arch includes the ectopterygoid (ECP), mesopterygoid (MSP), metapterygoid (MTP), and palatine (PAL). This terminology follows that of Weitzmann (1967). Elements of the palatine arch are essentially identical in all scopelarchids. Only the palatines bear teeth.

METAPTERYGOIDS: Each metapterygoid inserted between ventral shaft of hyomandibular, dorsal border of quadrate, and partly overlies



FIG. 7. Palatine arch and part of hyoid arch in *Scopelarchoides nicholsi*, SIO65-243, 103.2.

ventroposterior corner of mesopterygoid. Metapterygoids large, wellossified, forming a major brace between hyoid and palatine arches.

MESOPTERYGOID: Posterior section of each mesopterygoid bladelike, articulating with medial face of metapterygoid. Anteriorly each mesopterygoid splintlike, lying along dorsal border of ectopterygoid.

ECTOPTERYGOID: Ectopterygoid a large, elongate, strut-like bone, hollowed posteriorly forming a trough which receives anterior border of quadrate ventrally and ventral border of mesopterygoid dorsally. Ectopterygoid articulating with palatine anteroventrally and a splint-like portion of ectopterygoid lying along dorsal margin of palatine for about one-third of palatine length (fig. 7).

PALATINES: Palatines large, elongate, dentigerous bones, splintlike posteriorly and expanded anteriorly. Palatine teeth arranged irregularly in one or two rows, if in two rows medial teeth are the larger and at least anteriorly are large lanceolate canines (fig. 7). A broad dorsal projection on palatine bone articulates with cartilaginous core of lateral ethmoid and is attached by a ligament to the lateral ethmoid bone. An anteroventral head of the palatine articulates anteriorly with the vomer in a fossa provided for it.

Gosline et al. (1966) in an effort to differentiate inioms from "isospondylous" fishes, pointed out that in at least some inioms (Chlorophthalmus, Evermannella) a process from the anterior head of the palatine is directed upward and laterally, overlying the proximal end of the maxillary. The palatine projection was said to be supported by a lateral projection of the ethnioid. In "isospondylous" fishes (Tarpon, Yarella) the palatine typically has only a rounded elbow of bone overlying an area of the dorsomedial maxillary well removed from the proximal head of that bone. The authors point out that this character is not diagnostic, for the "isospondylous" fishes, Galaxias and Aplochiton, have an arrangement similar to the iniomous condition whereas Alepisaurus, Omosudis, and Sudis possess the character only in modified form, and Lestidium shows no articulation whatever between the anterolateral palatine and the maxillary. Paxton (1972) reported the "typical" iniomous condition to be lacking in myctophids. The palatine-maxillary arrangement in scopelarchids is somewhat intermediate between the iniomous and "isospondylous" conditions: no ossified area of the palatine overlies the maxillary, but a cartilaginous projection from the palatine articulates with a fossa in the maxillary. The point of this articulation is relatively distal to the proximal head of the maxillary.

Opercular apparatus.—

Bones of the opercular apparatus in scopelarchids include the opercle



FIG. 8. Opercular apparatus and hyoid arch in scopelarchids. A. Opercular apparatus, right side, lateral view. *Benthalbella elongata*, USC-E 1392, 126.1. B. Preopercle, right side, lateral view. *Scopelarchoides nicholsi*, SIO65-243, 103.2. C. Opercular apparatus, preopercle removed, left side, lateral view, *S. nicholsi* as above. D. Opercular apparatus, left side, lateral view, *Scopelarchoides signifer*, ORSTOM CYCLONE V-2, 104.6. F. Ventral portion of hyoid arch, basihyal detached, right side, lateral view, *B. dentata* as above.

(OP), subopercle (SOP), preopercle (POP), and interopercle (IOP).

OPERCLES: Each opercle a thin, in some species membranous, bone strengthened by a medial bony ridge expanding at the anterior margin of the opercle into a disk-shaped articulatory surface where the opercle is connected to the hyomandibular (fig. 8). Posterior margin of opercle strongly serrate in Scopelarchoides signifer and S. kreffti, and weakly so in S. danae and Rosenblattichthys volucris. Size of opercle relative to subopercle, as well as shape of both bones varies among species. In Scopelarchoides signifer, S. kreffti, S. climax, Rosenblattichthys, and Benthalbella, opercle essentially plow-share shaped (fig. 8) and equal to or smaller than subopercle. In these species pectoral insertion opposite a shallow to deep notch at opercle-subopercle border, except in B. dentata which exhibits a greatly expanded subopercle and in which pectoral insertion is opposite a notch in subopercle. In Scopelarchoides nicholsi, opercle greatly expanded, much larger than subopercle in size. In Scopelarchoides danae and Scopelarchus, opercle essentially rectangular, the vertical axis being the longer. Pectoral insertion in S. danae opposite a shallow indentation at opercle-subopercle border. Opercle in Scopelarchus distinctly larger than subopercle in size, pectoral insertion opposite a rounded notch in posterior border of opercle.

SUBOPERCLES: Subopercles thin, sometimes membranous, bones partly overlain dorsally by and connected to opercles. A wide connective tissue gap present between opercle-subopercle and preopercle in all scopelarchids but *Scopelarchoides danae* and species of *Scopelarchus* (fig. 8).

INTEROPERCLES: Each blade-like interopercle lying medially to ventral portion of preopercle and quadrate of each side. Interopercles well-separated from subopercles, to which they are connected loosely by connective tissue. Ligaments from interopercle of each side extend medially to interhyal, anteriorly to angular, and laterally and posteriorly through connective tissue to preopercle, quadrate, and subopercle. Interopercles Z-shaped in *Scopelarchoides signifer* and *Rosenblattich-thys volucris* and in the form of an inverted L in all other scopelarchids examined (fig. 8).

PREOPERCLES: Preopercles vertically elongate, expanded ventrally, carrying preopercular segment of preoperculomandibular cephalic sensory canal. Support of preopercle dorsally by hyomandibular and ventrally by posteroventral process of quadrate is discussed below. Sensory canal emerging onto bladelike expanded ventral portion of preopercle and passes to retroarticular process of articular. Ventral blade-like portion of preopercle noticeably expanded in posteroventral direction

in Scopelarchoides, Scopelarchus, and Rosenblattichthys, but not in Benthalbella (fig. 8).

Hyoid arch.-

The hyoid arch includes the following elements: basihval (BH), ceratohyal (CH), dorsal hypohyal (DHH), epihyal (EH), hyomandibular (HYOM), interhval (IH), quadrate (Q), symplectic (S), urohval (UH), and ventral hypohyal (VHH). All but the basihyal and urohyal are paired, one on each side. Confusion in nomenclature of the elements of the hyoid arch derives from uncertainties about the homologies of the various bones. Jollie (1962) recognized the hyomandibular as the serial homologue of the epibranchials, and used the terms ceratohyal anterior and ceratohval posterior for the elements between the hypohyals and interhval. Paxton (1972) followed Jollie's terminology. However, Nelson (1969), while agreeing that no serial homologue of the epibranchials supports the branchiostegal rays, suggested that the anterior and posterior ceratohyals of Jollie's terminology may actually represent serial homologues of the hypobranchials and ceratobranchials respectively, thereby requiring the coining of a new term for the hypohyals of conventional ichthyological nomenclature. Nelson adopted a neutral terminology, referring to the medial elements as the dorsohyal and ventrohyal, while the lateral elements were termed the anterohyal and posterohyal. Until new evidence is offered in resolution of this conflict. I choose to follow the established terminology of ichthyologists (e.g., Weitzmann, 1967; McAllister, 1968; Tominaga, 1968), while noting the existence of valid objections to this nomenclature. Except for the basibranchials, elements of the hvoid arch are essentially identical in all scopelarchids.

HYOMANDIBULAR: Hyomandibular exhibiting two stiff flattened rods of bone dorsally, anterior rod articulating with a fossa in sphenotic, the posterior with a fossa in pterotic, and a thin sheet of bone connecting the two rods. In *Scopelarchoides, Benthalbella*, and *Rosenblattichthys*, hyomandibular composed of four main rods of bone roughly forming an "X," including the two dorsal articulating rods, a ventral shaft articulating with symplectic and interhyal, and a posterior arm articulating with and supporting the opercle. In *Scopelarchus* posterior rod replaced by a rounded ridge of bone, rather than a discrete flattened rod, and provided posteriorly with an articulating head for the opercle. A stout ridge of bone extending along main dorsoventral axis of hyomandibular closely connects with and supports preopercle. A thin sheath of bone extending anteriorly from hyomandibular articulating with and partly covering medial face of metapterygoid. SYMPLECTIC: Symplectic an elongate well-ossified splint, a little thicker dorsally, articulating with medial face of posteroventral process of quadrate (fig. 7). Level of hyomandibular-symplectic joint on about same level as quadrate-metapterygoid joint.

QUADRATE: Quadrate lying ventral to metapterygoid and composed of usual three main parts: body, posteroventral process, and articular head. Body delta-shaped, articulating dorsally via a synchondral joint with metapterygoid, and fitting anteriorly into a trough-like depression on the posterior surface of the ectopterygoid. Posteroventral process receiving preopercle and symplectic medially. Articular head bearing two strong condyles, one lateral and one medial, with a concave surface between receiving the convex articular surface of retroarticular process.

INTERHYAL: Interhyal rod-like dorsally and flattened, rounded, and somewhat expanded ventrally (fig. 8). Interhyal bound by ligaments dorsally to hyomandibular-symplectic joint and ventrally to posterior articular facet of epihyal.

EPHHYAL: Epihyal stout and wedge-shaped, articulating via synchondral joint with ceratohyal.

CERATOHYAL: Ceratohyal similar to epihyal in shape, articulating anteriorly with hypohyals. Paxton (1972) reported a ceratohyal foramen in the myctophids *Notolychnus valdiviae* and *Triphoturus mexicanus*. The ceratohyal foramen, a characteristic feature of beryciform fishes, is lacking in scopelarchids.

HYPOHYALS: A dorsal hypohyal and slightly larger ventral hypohyal present anterior to ceratohyal. A ventroanterior knob on ventral hypohyal connected via a strong ligament to corresponding fork (left or right) of yoke-like anterior projection of urohyal.

BRANCHHOSTEGAL RAYS: Eight branchiostegal rays are present in all scopelarchids, are acinaciform, and are distributed in the 4 + X, actually 4 + 4, pattern described by McAllister (1968), with the epihyal branchiostegals external and possessing a broader head than the ventral or internal ceratohyal branchiostegals.

UROHYAL: Urohyal elongate, blade-like, irregularly shaped but deeper posteriorly, possessing anteriorly a rod-like structure split into right and left projections, as in a yoke, with each lateral prong connected by a ligament to corresponding ventral hypohyal.

BASHHYAL: Nelson (1969) discusses at great length confusion in the literature derived from failing to distinguish between endoskeletal and dermal components of the basihyal and gill arches. Although lengths of the relative elements as well as degree and extent of dentition vary in scopelarchids, the basibranchial series in all consists of three copulae (following Nelson's terminology): basihyal, basibranchials 1-3, and a posterior cartilaginous copula receiving elements of the fourth and fifth gill arches. Nelson states the primitive condition of dermal tooth plates associated with these copulae, exhibited by both *Elops* and *Aulopus*, is that in which there is a toothplate over the basihyal, and a second, more elongate, undivided, toothplate over basibranchials 1-3. This is true of all scopelarchids. However, the degree of tooth development upon these dermal plates is variable, and appears to be directly related to the length of the basihyal. In the discussion that follows, the lingual teeth of scopelarchids will be referred to as basihyal or basibranchial teeth for the sake of brevity, but the dermal as opposed to endochondral origin of the tooth plates should be noted.

In all larval scopelarchids, lingual teeth first appear on the elongate basihyal, but the length of the basihyal and rearward extent of basibranchial teeth depends upon the species involved.

Lingual teeth are restricted to an elongate basihyal (except for 1-2 small, possibly replacement teeth over the anterior end of the first basibranchial) in *Benthalbella, Scopelarchoides signifer, S. climax,* and *S. kreffti.* The basihyal is considerably shortened, and lingual teeth occur over the first two or three basibranchials in *Rosenblattichthys, Scopelarchus,* and *Scopelarchoides nicholsi* and *S. danae* (fig. 9). However, the combined number and length of the lingual row of teeth, whether restricted to the basihyal or present over the basibranchials as well, is about the same in all scopelarchids (fig. 9).

Branchial arches.—

Terminology employed for the various elements of the branchial arches follows that of Nelson (1969). Endoskeletal components include the following: basibranchials (bb), ceratobranchials (cb), epibranchials (eb), hypobranchials (hb), and infrapharyngobranchials, here referred to simply as pharyngobranchials (pb). Dermal elements associated with these bones include two types of dentition: (a) gill tooth plates developing as small nodules of bone on the laterodorsal margin of hypobranchials 1-2; ceratobranchials 1-3 (in some 1-4); epibranchials 1-2 (in some 1-3); nodules expanding with growth forming flattened plates of bone bearing one-to-many small teeth arranged in one-to-three rows on dorsal margin of plate; number of gill tooth plates, number of teeth per plate, and number of rows of teeth per plate varying nonuniformly with size, number of plates increasing (up to a certain point) with size, but with increasing size some of the plates fuse, making any counts of number of bases or number of teeth per base valueless as a systematic character;



FIG. 9. Lingual teeth and branchial arches in scopelarchids. A. Basihyal teeth, *Scopelarchoides signifer*, ORSTOM, CYCLONE V-2, 104.6. B. Basihyal and basibranchial teeth in *Rosenblattichthys volucris*, LACM 9806, 103.5. C. Branchial arches and basihyal (fifth ceratobranchial not shown), *Benthalbellaelongata*, USC-E 1392, 126.1. D. Basihyal and basibranchial teeth, *Scopelarchus guentheri*, S1069-21, 112.4. E. Basihyal and basibranchial teeth, *Scopelarchoides danae*, S1061-584, 89.1.

(b) conical teeth, so termed for convenience in distinguishing the larger single-based teeth of gill arches from the gill teeth. Conical teeth invariably present on pharyngobranchials 3-4, epibranchials 2-3, ceratobranchial 5, and sometimes present on pharyngobranchial 2.

All bones bearing conical teeth are no doubt compound elements with the dermal dentigerous element fused with the endoskeletal component (Nelson, 1969). Nelson (1969, pp. 488-490) has discussed in detail the controversy over homologies and applicable terminology to be applied to these compound elements, especially the most posterior element, which in scopelarchids is by far the largest and bears the most elongate conical teeth of any branchial arch element. This large element is largely



FIG. 10. Branchial arches in *Scopelarchoides signifer*, ORSTOM, CYCLONE V-2, 104.6.

posterior to and unsupported by the fourth pharyngobranchial. I follow Nelson's terminology for these elements.

BASIBRANCHIAL SERIES: Lingual teeth variously present or absent over the basibranchial series have been already discussed. A dermal plate invariably overlying basibranchials 1-3, with no sign of sutures over cartilaginous joints between basibranchials 1-3, similar to the condition described from myctophids by Paxton (1972). Posterior to third basibranchial a cartilaginous area, apparently single and median, representing third copula of basibranchial series according to Nelson (1969), receives articular heads of fourth and fifth ceratobranchials.

HYPOBRANCHIALS: There are three paired hypobranchials corresponding to the first three gill arches. Hypobranchials 1 and 2 (fig. 10) articulating in cartilaginous areas between basibranchials 1-2 and 2-3 respectively. Third hypobranchials shorter but thicker than first two pairs, attached to posterior section of third basibranchial and parallel it along half its length. Third hypobranchials exhibiting an anterior process converging anteroventrally with its fellow of the opposite side. Third hypobranchials cartilaginous posteriorly, articulating laterally with third ceratobranchials and medially with third, cartilaginous copula [following Nelson's (1969) terminology].

CERATOBRANCHIALS: There are five paired ceratobranchials. Ceratobranchials 1-4 essentially identical in shape, articulating dorsally with corresponding epibranchial. Ceratobranchials 1-3 articulating ventrally with corresponding hypobranchial. Ceratobranchials 4-5 articulating ventrally with third cartilaginous basibranchial copula. Fifth ceratobranchial, or lower pharyngeal, a compound dermal-endoskeletal element, bearing a strong row(s) of conical teeth on dorsal surface and connecting via a long ligament to ventral end of fourth epibranchial.

EPIBRANCHIALS: The epibranchials and pharyngobranchials are similar in *Scopelarchoides signifer* (and presumably *S. climax* and *S. kreffti*), *Rosenblattichthys alatus* and *R. volucris* (and presumably *R. hubbsi*), and *Benthalbella*. The pattern in these fishes will be described first, followed by an account of the changes that take place in the lineage leading to *Scopelarchus*.

Epibranchial of first arch an elongate, Y-shaped bone, connecting dorsally with a short, rodlike suspensory (first) pharyngobranchial. A projection from first epibranchial connecting via a ligament with a similar hook-shaped projection on second pharyngobranchial (fig. 11). Second epibranchial with dorsolateral keel along ventral one-half of length and a short articulatory projection at about midlength, connecting with distal end of second pharyngobranchial. Second epibranchial overlies and connects to third pharyngobranchial medially. Second pharyngobranchial extending to anterior end of third pharyngobranchial, and connecting with it via a ligament. Third epibranchial connecting medially with posterior end of third pharyngobranchial. A dorsolateral keel present on ventral half of third epibranchial. Fourth epibranchial stout, enden-



FIG. 11. Diagrammatic representation of the changing point of support of first epibranchial in scopelarchid species. Second pharyngobranchial indicated by black coloration. A. Scopelarchoides signifer, ORSTOM CYCLONE V-2, 104.6. B. S. nicholsi, SIO65-243, 103.2. C. S. danae, SIO61-584, 89.1. D. Scopelarchus guentheri, SIO69-21, 112.4.

tate, articulating medially with fourth pharyngobranchial through cartilage. A strong dorsolateral keel on fourth epibranchial.

In Scopelarchoides nicholsi and S. danae the third and fourth epibranchials are similar to other scopelarchid species, but S. nicholsi, S. danae, and the species of Scopelarchus lack a suspensory pharyngobranchial, and exhibit important changes in the support of the first epibranchial (fig. 11).

In *S. nicholsi* the first epibranchial and second pharyngobranchial remain Y-shaped, and a ligament connects the hooks of the Y of each bone. The first epibranchial finds its support dorsally on the medial one-third of the second pharyngobranchial, to which it is connected via a ligament (fig. 11). In all scopelarchids the connections of the second pharyngobranchial with the second epibranchial and third pharyngobranchial remain the same.

In S. danae and Scopelarchus, the hook-like projections of both the first epibranchial and second pharyngobranchial are lost, and in S. danae support for the dorsal end of the first epibranchial is found at about the middle of the second pharyngobranchial (fig. 11).

Finally, in the species of *Scopelarchus* support for the first epibranchial is found at the point of articulation between the second pharyngobranchial and the second epibranchial. Any functional significance of these changes, i.e., the loss of the suspensory pharyngobranchial and the shifting point of support of the first epibranchial, remains unclear to me.

PHARYNGOBRANCHIALS: Relationships and fate of first and second pharyngobranchials are discussed above. Pharyngobranchial (upper pharyngeal bone) of third arch a compound element of endoskeletal and dermal origin, providing principal dorsomedial support for first three branchial arches, and supplied with strong conical teeth in one or more rows. Posteriorly third pharyngobranchial connecting via cartilage with fourth pharyngobranchial. Fourth pharyngobranchial a small cartilaginous element receiving dorsally the articular head of the fourth epibranchial. Fourth and fifth upper pharyngeal tooth plates enlarged, rounded, and supporting large conical teeth. Fifth upper pharyngeal plate much the larger.

The possible homologies of the fifth upper pharyngeal plate are discussed by Nelson (1969, pp. 488-490).

Vertebrae, supraneurals, intramuscular bones, and caudal skeleton.-

VERTEBRAE: The number of vertebrae in scopelarchids varies between 40 and 65: Benthalbella (54-65), Rosenblattichthys (46-51), Scopelarchoides(45-56), Scopelarchus (40-51). The point of separation between precaudal and caudal vertebrae is taken as the first centrum with a complete haemal arch being termed the first caudal vertebra. This could not be determined from radiographs in most cases, and probably varies slightly in ontogeny. No attempt was made to separate most vertebral counts in this fashion. For cleared and stained material the following precaudal + caudal vertebral counts were obtained: Benthalbella elongata (21 + 43 = 64); B. dentata (20 + 34 = 54); B. infans (22 + 36 = 58); B. macropinna (16 + 45 = 61); Rosenblattichthys volucris (17 + 32 = 49); Scopelarchoides danae (18 + 31 = 49); S. nicholsi (16 + 29 = 45); S. signifer (16 + 33 = 49); Scopelarchus analis (18 + 29 = 47); S. guentheri (18 + 29 = 47); S. michaelsarsi (13 + 27 = 40).



FIG. 12. Vertebrae, intramuscular bones, and caudal skeleton. A. Precaudal vertebrae 1-3, *Benthalbelia elongaia* USC-E 1392, 126.1. B. Precaudal vertebrae 1-3, *Scopelarchoides nicholsi* S1065-243, 103.2. C. Precaudal vertebrae 13-16, and first caudal vertebra, *Scopelarchoides nicholsi*, as above. D. Caudal vertebra (26th vertebra, 10th caudal) *S. nicholsi*, as above. E. Caudal skeleton, *Scopelarchus analis*, UH 70/9/12, 95.0. F. Caudal skeleton, *Benthalbelia dentata*, S1063-379, 118.0.

EP, epural; HYP, hypural; PAR, parhypural; PU, preural centrum; SM, supraneural; U, ural centrum; UN, uroneural.

Each precaudal centrum, except the first half-centrum, large, amphicoelous, pierced by a large notochord canal. First several centra lacking neural spines as neural arches not fused dorsally until fifth to tenth centrum.

Intramuscular bones present in all scopelarchids (cf., Gosline et al., 1966, p. 11). A detailed, centrum-by-centrum, species-by-species analysis of intramuscular bones was not attempted due to the poorly ossified state of a number of the smaller specimens. Intramuscular bones are described below from material of *Benthalbella elongata* and *Scopelarchoides nicholsi*, and probably are indicative of the typical scopelarchid arrangement of these bones (fig. 12).

First and second vertebrae each bearing an epineural and epicentral. In *B. elongata* an additional intramuscular bone attached to epicentral of second centrum somewhat distal to attachment of epicentral to centrum. On vertebrae succeeding second vertebra, elements corresponding to epineural become epicentral in point of attachment until posterior to anal fin origin when position of corresponding elements shifts again dorsally and succeeding elements are epineural. Third and succeeding centra (all counts from anterior to posterior) bearing parapophyses, one on each side, each supporting one ventral (pleural) and two dorsal (epipleural) ribs (only one epipleural in S. nicholsi). In B. elongata epipleurals separating vertically in point of attachment after last centrum with pleural rib (eleventh vertebra), the dorsal element becoming epicentral. Thereafter each vertebrae supports three intramuscular bones, one or two epicentrals (dorsal epicentral becoming an epineural after anal fin origin). and an epipleural. Posteriorly epipleural shifting ventrally in position becoming an epihaemal. Far posteriorly all three elements connected to vertebrae only through connective tissue, and in the one specimen of B. elongata examined, no intramuscular bones are visible posterior to the fiftieth (out of 64) centrum. S. nicholsi is similar in all respects except that only a single epipleural element is present, but this element shifts ventrally on posterior succeeding vertebrae, becoming an epihaemal as in *B. elongata*. In all scopelarchids the parapophyses expand posteriorly (on succeeding centra) to form haemal arches and eventually a haemal spine on the first caudal vertebra.

SUPRANEURALS: Supraneurals invariably three, the first inserted between neural arch elements of the first vertebra (invariably a halfcentrum), succeeding supraneurals all in advance of anterior proximal radial of dorsal fin, vary in point of insertion depending upon the number of precaudal vertebrae. CAUDAL FIN: Gosline (1960) and Nybelin (1963) presented differing terminologies for elements of the caudal fin skeleton of teleosts. In designating hypurals and centra I follow Nybelin, for despite several resulting difficulties (discussed by Paxton, 1972), Nybelin's morphologically based terminology has gained wide acceptence (Gosline, 1965; Weitzmann, 1967; Greenwood, 1968; Monod, 1968; Patterson, 1968; Tominaga, 1968; Goody, 1969; Rosen and Patterson, 1969).

The caudal fin skeleton of *Scopelarchoides nicholsi* has been figured by Rosen and Patterson (1969) and I have included figures of the caudal skeletons of *Benthalbella dentata* and *Scopelarchus analis* (fig. 12). Terminal preural vertebra (PU₁) and ural vertebra (U₁ + U₂) fused (Rosen and Patterson, 1969). No independent second ural ossification (U) exists in scopelarchids, although such an element is visible in at least some paralepidids. A large parhypural and six hypurals support the 1 + 9 + 8 + 1 (counting from dorsal) principal caudal rays. There are three epurals (except *B. dentata* which has only two) and two uroneurals, the distal pair thin plates applied over dorsoposterior surface of the stegural.

Dorsal fin.-

Scopelarchids exhibit a range of 5-10 dorsal rays. Last dorsal ray divided completely to base and counted as one element. Number of pterygiophores is equal to number of fin rays, but whereas the first pterygiophore supports the first two rays, the last two pterygiophores support the last divided ray. Anterior part of anteriormost proximal radial more advanced with respect to vertebral column in short-bodied species than in more elongate species. In the following listing the numbers in parentheses indicate the vertebral numbers over which the anteriormost part of the first pterygiophore inserts: *Scopelarchus michaelsarsi* (7-8); *S. analis* (8-9); *S. guentheri* (8-9); *Scopelarchoides nicholsi* (8-9); *S. signifer* (8-9); *S. danae* (9-10); *Rosenblattichthys volucris* (9-10); *Benthalbella macropinna* (10-11); *B. dentata* (13); *B. infans* (13-14); *B. elongata* (14-15), all based on cleared and stained material only.

First pterygiophore consisting of an elongate keel-like proximal radial (PR) (fig. 13) and two distal radials (DR) supporting first two fin rays (FR). All distal radials consisting of a spherical cartilage with two lateral caps of bone where distal radials articulate with basal part of fin rays. Second and in most species third pterygiophore consisting of proximal and distal radials only. In *Benthalbella, Scopelarchoides signifer,* and *Rosenblattichthys volucris* pterygiophores succeeding first two or three consisting of separate proximal, medial, and distal radials, except for terminal two pterygiophores. In specimens examined of all other species, no medial radials (MR) are visible. Final two pterygiophores separate ventrally but



FIG. 13. Dorsal and anal fins in *Rosenblattichthys volucris*. LACM 9806, 103.5. A. Dorsal fin, left lateral view. **B**. Dorsal fin, posteriormost fin rays, left lateral view. **C**. Anal fin, posteriormost fin rays, right lateral view. **D**. Anal fin, anteriormost fin rays, right lateral view.

connected by cartilage or bone dorsally, medial radials absent in most species examined, but a single distal radial supporting the last divided ray is present.

Anal fin.—

Scopelarchids possess 17-39 anal rays. Last anal ray divided completely to base and counted as one element. Number of pterygiophores equal to number of fin rays but the first pterygiophore supports the anterior first two rays whereas the final two pterygiophores support the last divided ray. Anteriormost part of anterior proximal radial inserted more anteriorly with respect to vertebral column in short-bodied than in elongate species. In the following listing the numbers in parentheses indicate the vertebral numbers under which the anteriormost part of the anterior proximal radial inserts: *Scopelarchus michaelsarsi* (18-19); *Scopelarchoides signifer* (18-19); *S. nicholsi* (20-21); *Scopelarchus guentheri* (20-21); *S. analis* (20-21); *Scopelarchoides danae* (21-22); *Rosenblattichthys volucris* (24-25); *Benthalbella macropinna* (25-26); *B. dentata* (28-29); *B. infans* (31-32); *B. elongata* (32-33), all based on cleared and stained material only.

First pterygiophore consisting of an elongate keel-like proximal radial and one distal radial supporting the first and second anal rays.



F1G. 14. Pectoral girdle in scopelarchids. A. Right lateral view, *Scopelarchoides* nicholsi, S1O65-243, 103.2. B. Right lateral view, *Benthalbella elongata*, USC-E 1392, 126.1. C. Extrascapular bones, left lateral view, *Rosenblattichthys volucris*, LACM 9806, 103.5.

Distal radials of anal fin similar to those of dorsal. Second pterygiophore consisting of a proximal and distal radial supporting third anal ray. Succeeding pterygiophores consisting of proximal, medial, and distal radials. Final pterygiophores partly united, consisting of two proximal radials, and a single medial and single distal radial support the last completely divided anal ray.

Pectoral girdle.—

The dermal elements of the pectoral girdle include the posttemporal (PT), supracheithrum (SCL), cleithrum (CL), and two postcleithra, the dorsal (DPCL) and ventral (VPCL). Endochondral elements include the scapula (SC) and coracoid (COR). Two (or three) extrascapulars (ESC) are associated with but not part of the pectoral girdle. My terminology for these elements is that more or less standard among ichthyologists (Paxton, 1972; Rofen, 1966; Tominaga, 1968; Weitzmann, 1967).

POSTTEMPORAL: Posttemporal of scopelarchids not forked as in myctophids (Paxton, 1972) or omosudids (Rofen, 1966b) but consisting

of two portions: (a) a rod-like dorsal articulating process, and (b) a ventral rounded blade-like portion. Dorsal process of posttemporat converging medially with its fellow of the opposite side and is connected via a ligament to the epiotic. Ventral portion partially covering dorsal portion of supracleithrum and in most cases is itself partly covered by second extrascapular anteriorly. A raised tube-like area of bone on posttemporal encases laterosensory canal which posttemporal receives from second extrascapular and passes to supracleithrum. A strong ligament connecting medial face of posttemporal to opisthotic.

EXTRASCAPULARS: There are two extrascapulars in all scopelarchids except *Rosenblattichthys* as noted below (fig. 14). Extrascapulars somewhat irregularly shaped but usually at least partly troughlike, and usually pierced by pores. Second (posteriormost) extrascapular always the larger. Three branches of the laterosensory system meet at the second extrascapular: the temporal branch from the pterotic, a supratemporal branch from the first extrascapular, and the main branch of the lateral line canal. Cephalic laterosensory canals of scopelarchids agree well with those of other inioms (Gosline et al., 1966, pp. 3-4). In *Rosenblattichthys volucris* there is apparently a third extrascapular, lying between the second extrascapular and the posttemporal. This extra element is a pierced, rounded, scale-like bone. Its presence or absence in *R. alatus* and *R. hubbsi* is unknown.

SUPRACLEITHRUM: Supracleithrum an elongate, straight, flattened bone partly overlain by the posttemporal dorsally and partially overlying the cleithrum ventrally. A raised tube of bone on the supracleithrum passes the laterosensory canal from the posttemporal to the lateral line.

CLEITHRUM: Cleithrum the largest and most complex element of the pectoral girdle. Main shaft of cleithrum forming a moderately arched curve of thickened bone ending dorsally in a rod-like shaft lying beneath the supracleithrum. Ventral to this dorsal shaft is a thin shelf of bone, the posterior lamina, lying above the scapula and supporting the small, rounded, dorsal postcleithrum medially. Ventral portion of main shaft of cleithrum exhibits a bony flange at about midlength articulating with scapula and dorsal anterior margin of coracoid. Ventrally the main shaft of the cleithrum curves anteriorly, and slightly medially, converging with its fellow of the opposite side, to which it is strongly connected by ligaments, near the ventral midline beneath the pharynx.

SCAPULA: Scapula nearly triangular, articulating dorsally and anteriorly with cleithrum, and ventrally with coracoid. A saddle-shaped ridge on scapula supporting enlarged dorsalmost pectoral ray. Scapula completely supporting first (dorsalmost) pectoral proximal radial and partly supporting second proximal radial. A large central foramen piercing scapula. Inioms lack a mesocoracoid.

CORACOID: Coracoid an expanded sheet of bone rounded concavely at anterior margin and convexly at posterior margin, narrowing to a short rod-like process anteroventrally and strongly connected via ligaments to ventral tip of cleithrum. Coracoid articulating anterodorsally with cleithrum, but a moderate to extensive coracocleithral fenestra separates the two bones over most of length of coracoid. In *Scopelarchoides. Scopelarchus*, and *Rosenblattichthys*, coracoid widely expanded, and coracocleithral fenestra correspondingly small, but in *Benthalbella* coracoid relatively narrow, and coracocleithral fenestra noticeably enlarged. Coracoid supports third and fourth proximal pectoral radials, but second proximal radial usually at scapulocoracoid border.

PECTORAL PROXIMAL RADIALS: There are four proximal pectoral radials in scopelarchids, each approximately hour-glass-shaped. Splint-like ventral postcleithrum lying medial to three ventral proximal radials.

Parr's (1929, p. 15) statement that *Scopelarchoides* differs from *Scopelarchus* in that (among other characters) the fourth proximal radial attaches to the coracoid via a narrow head inserted into a semicircular emargination on the coracoid is true for *Scopelarchoides nicholsi, S. signifer,* and to a lesser degree *S. danae.* This condition is also seen in *Rosenblattichthys volucris* and to a lesser extent in *Benthalbella infans.* In all other species examined the connection of the fourth radial with the coracoid was broad-based, without any emargination of the coracoid.

A row of distal cartilaginous radials, one per ray, is found between the bases of the pectoral fin rays, which number 18-28 in the Scopelarchidae.

Pelvic girdle.—

My terminology for pelvic girdle structures follows that of Gosline (1961), Gosline et al. (1966), Weitzmann (1967), and Paxton (1972). Pelvic bones (fig. 15) paired, flattened, elongate, lying in ventral plane of abdominal body wall, and not reaching to nor connected with the pectoral girdle. Anterior region of each pelvic bone consisting of a thick lateral strut supporting a thin medial wing of bone. Each strut converging in midline anteriorly with its fellow of the opposite side, and strongly connected to it. Posteriorly pelvic bones consist of two portions: (a) a lateral expanded area of strong bone providing on its lateral surface support for the nine moveable pelvic rays; (b) a medial area of two thin bony lamellae encasing a cartilaginous plate. Cartilaginous plates of each side coalescing posteriorly forming a common cartilaginous pelvic plate.



FIG. 15. Pelvic girdle of scopelarchids. A. First pelvic ray of left pelvic fin, posterior view, dorsal portion of fin to left of diagram, *Benthalbella elongata*, USC-E 1392, 126.1. B. Pelvic bones, ventral view, *B. elongata* as above. C. Pelvic bones, *Rosenblattichthys volucris*, LACM 9806, 103.5.

Pelvic plate on posteroventral surface exhibiting a short to moderately elongate knob of cartilage connected by connective tissue to abdominal cavity wall. Thus pelvic bones, being separate for one-half or more of their respective lengths, are bound firmly together, anteriorly by connective tissue and posteriorly by cartilage. Medial plates of bone in posterior area of pelvic girdle exhibiting transverse thickenings or struts of bone abutting one another in midline in *Scopelarchoides signifer* and *Rosenblattichthys volucris*.

The pelvic rays are numbered in order from lateral to medial. There are two bony or cartilaginous radials: the first between the expanded bases of the first stout ray, the second between the bases of the third to fifth rays. The sixth to eighth rays are supported ventrally by the expanded base of the ninth (innermost) ray, which Gosline (1961, pp. 20-21) pointed out is a compound element consisting of the base of the innermost ray fused with the innermost pterygiophore. I have seen no sign in scopel-archids of the curved splint of bone along the outer surface of the upper half of the outermost ray recorded by Gosline (1961, p. 18) for *Solivomer* (Neoscopelidae) and by Paxton (1972, p. 32) for most myctophids.

JOHNSON: SCOPELARCHIDAE

ARTIFICIAL KEY TO THE GENERA OF SCOPELARCHIDS (ADULTS)

1A	. Distinct, equal or subequal stripes of pigment above and below the lateral
	line, extending forward from the caudal peduncle; pectorals exceed pelvics in length
	[pectoral rays 18-22, no marked concentration of pigment on upper lobe of caudal
	fin] Scopelarchus Alcock 1896
1B.	Distinct stripes of pigment above or below lateral line absent, or if present, markedly
	unequal, with pigment concentrated either above or below lateral line; pectorals
	equal to (one species) or distinctly less than pelvics in length [pectorals exceed
	pelvics in length in Scopelarchoides signifer which has 22-25 pectoral rays, a marked
	concentration of pigment on upper lobe of caudal fin, and no pigment stripes]2
24	(1B) Pelvic insertion distinctly in advance of vertical through base of first dorsal fin
2.7 %	ray
20	Pelvic insertion distinctly behind a vertical through base of first dorsal ray feither
20.	marked etrines of nigment especiated with leteral line or anal rays 25 or more or
	hat keu stripes of pignent associated with lateral line of anal rays 25 of more, of
	both j
3A	(2A). Lingual teeth occurring over first two or three basibranchials as well as over
	basihyal; lateral line scales 47-53; vertebrae 46-51. [no stripes of pigment associated
	with lateral line; anal rays 20-24] Rosenblattichthys Johnson 1974
3B.	Lingual teeth occurring only over basihyal or at most 1-2 small teeth over anterior
	end of first basibranchial; lateral line scales 54 or more: vertebrae 54 or more 4
4A	(3B). Pigment stripes along lateral line present Scopelarchoides kreffti Johnson 1972
4B.	Pigment stripes along lateral line absent Benthalbella Zugmayer 1911

ARTIFICIAL KEY TO THE GENERA OF SCOPELARCHIDS (Larvae, 20 mm. and larger)

1A. Peritoneal sections absent; origin of pelvic fin buds ventrolateral and distinctly ahead
of vertical through base of first dorsal ray [except B. macropinna, which has 35 or
more anal rays, anal origin at midlength, and 5-6 dorsal rays]: accessory pigment
spots or areas absent
1B. Peritoneal sections present, origin of pelvic fin buds distinctly behind dorsal origin,
accessory pigment spots or areas present or absent
2A (1B). Accessory pigment spots or areas distinctly present, origin of pectoral fin buds
midlateral in abdominal body wall, above level of intestine
2B. Accessory pigment spots or areas absent, origin of pectoral fin buds ventrolateral, at
or below level of intestine Scopelarchus Alcock 1896
3A (2A). Middorsal and midventral accessory pigment areas distinctly anterior to a vertical
through end of adipose and anal bases, respectively, one peritoneal section only
[presumed for R. hubbsi] Rosenblattichthys Johnson 1974
3B. Middorsal and midventral accessory pigment areas and spots (DA, PA) distinctly
posterior to vertical through end of adipose and anal bases respectively, one or
three peritoneal sections [presumed for S. kreffti] Scopelarchoides Parr 1929

Benthalbella Zugmayer 1911

Benthalbella Zugmayer, 1911a, p. 14. Neoscopelarchoides Chapman, 1939, p. 530.

Type Species-Benthalbella infans Zugmayer 1911.

Diagnosis—Scopelarchids with parietals present, antorbital absent (except *B. macropinna*), ethmoid process on first infraorbital absent, basihyal elongate; lingual teeth restricted to over basihyal, or at most 1-2 small teeth over anterior end of first basibranchial; suspensory pharyngobranchial present; coracoid not much expanded, coracocleithral fenestra large; 54-65 vertebrae; 54-66 lateral line scales; dermal pigment stripes absent; pelvic insertion well in advance of dorsal origin; larvae lacking peritoneal pigment, accessory pigment spots or areas, dermal pigment stripes, and reaching large size 50-90 mm., prior to metamorphosis or appearance of any pigment on body.

Description.—Frontals not greatly expanded posteriorly, restricted to anterior one-third of postorbital dorsal skull roof; supraoccipital spine long and spike-like; opisthotics lacking anteroventrally directed projection; sagitta small; supramaxilla small and splintlike (except *B. macropinna*); opercle plowshare shaped, subequal to or less than subopercle (subopercle considerably expanded in *B. dentata*); wide connective tissue filled space between opercle-subopercle and preopercle; hyomandibular with four rod-like arms; two extrascapulars; three epurals except only two in *B. dentata*.

Dorsal rays 5-10, anal rays 17-39, pectoral rays 19-28, lateral line scales 54-66, vertebrae 54-65.

Large-bodied scopelarchids, all but B. infans reaching over 200 mm. in length, body elongate, moderately shallow to quite deep, moderately to strongly compressed. Belly straight with low scaly ridge of skin at midventral line between pelvic and anus, and between POp and AO luminous organs in Benthalbella infans. Anus moderately in advance of anal origin. Body scales behind pectoral insertion not noticeably larger than adjacent body scales. Lateral line scale above anal origin: height of scale less than length (B. infans, B. linguidens, B. elongata) or slightly greater than length (B. macropinna, B. dentata). Tympanum height moderate (except relatively deep in B. macropinna). Dense patch of papillae on each side of snout medial to nasals. Eyes large, tubular, directed straight upward except directed dorsoanteriad in B. dentata. Pearl organ a dorsally and ventrally flattened oval. Pelvics abdominal, inserted well in advance of dorsal origin in adults. Pelvic rays stouter than pectoral rays, pelvic length slightly to greatly exceeding pectoral length. Body color for most part a dull uniform brown with slightly heavier pigmentation emphasizing scale pockets. Pigment present evenly on all fins. No dermal pigment stripes.

Larvae with extremely elongate shallow body with shallow peduncle. Dorsal and ventral adipose fins remain elongate until metamorphosis.
Post-pelvic gut length remains short until metamorphosis. Origin of pelvic fin buds ventrolateral, well ahead of dorsal in all but *B. macropinna* where they appear beneath dorsal base. Peritoneal pigment or sections absent in larvae. Accessory pigment spots or areas absent. Dermal pigment stripes absent. No pigment on body prior to metamorphosis.

Discussion.-Metamorphosis in Benthalbella spp. is postponed. Larvae grow to a large size while retaining larval characteristics (figs. 17, 18). In all other scopelarchid genera peritoneal pigment appears early (based on size) in larval life and occurs as one to three discrete sections. Adult characters in other scopelarchid larvae are acquired essentially one by one over an increment of 20-40 mm. of growth. All species have peritoneal pigment in larvae larger than 20-22 mm, in size, and most over 33 mm, possess pigmentation on the body, usually expressed as dermal stripes above or below the lateral line. In Benthalbella, the larvae achieve large size [minimum size records for earliest metamorphic specimens (in mm.): B. dentata (49.6); B. elongata (89.1); B. infans (55.1); B. linguidens, no metamorphic specimens known, but largest larval specimen (85.5) still retains all larval characteristics; B. macropinna (65.1)], prior to metamorphosis. Metamorphosis when it occurs is rapid (over a size increment of 10 mm, in *B. dentata*, see fig. 18) and adult characters appear with near synchrony over a very short increment of growth. Concurrent with the first appearance of peritoneal pigment, which does not occur in discrete sections as in other scopelarchids, is the rapid elongation of the intestine bringing the anus to its adult position directly in front of the anal fin, the rapid posterior expansion of the caecum, extending to just before the anus, appearance of gonad, investiture of the abdominal cavity wall with muscle, appearance of body and head pigmentation, and appearance of scales, producing over a short increment of growth a young but essentially adult individual. This pattern of rapid metamorphosis is, as far as is known, unique to Benthalbella.

KEY TO THE SPECIES OF Benthalbella

Benthalbella dentata (Chapman) 1939. Figure 16.

Neoscopelarchoides dentatus Chapman, 1939, p. 530; Follett, 1952, p. 412; Mead and Bohlke, 1953, p. 244; Marshall, 1955, pp. 310, 314; Ebeling, 1962, p. 141; Pearcy, 1964, p. 87; McAllister, 1968, p. 95.

Benthalbella dentata: Berry and Perkins, 1966, p. 665; Bussing and Bussing, 1966, p. 59; Fitch and Lavenberg, 1968, p. 52.

Holotype-USNM 108145. 162 mm. TL-C. Eastern North Pacific 56° 22' N, 145° 54' W, 27 January, 1929.

Comparative diagnosis.—A species of Benthalbella with 6-8 (usually 6-7) dorsal rays, 17-20 anal rays, 21-24 pectoral rays, and 54-58 lateral line scales. The combination of these characters distinguishes *B. dentata* from all other known species of scopelarchids.

Description.—Based on 89 (20.0-54.7) larvae, 7 (49.6-57.1) metamorphosing specimens, and 24 (56.5-203.0) adolescents and adults. With the exception of meristic characters, the description given first is that of adults, followed by an account of development.

MERISTIC CHARACTERS: Values for the holotype (from Chapman, 1939) given in parentheses. Dorsal 6-8 (7), anal 17-20 (20), pectoral



FIG. 16. Benthalbella demaia (Chapman). A. Adult, SIO71-15, 148.0. B. Lateral line scale above anal origin, SIO67-104, 151.8. C. Lateral line scale above pectoral insertion, LACM 9621, 198.0. D. Penultimate lateral line scale, LACM 9704, 146.6.

21-24 (23), lateral line scales 54-58 (56), vertebrae 54-55. Chapman (1939) reported anal fin counts from some specimens as high as 21, and pectoral counts as high as 25.

PROPORTIONAL DIMENSIONS: Based on 10 (97.1-198.0) specimens: LACM 9253, 1 (95.8); LACM 9364, 1 (111.5); LACM 9365, 1 (164.1); LACM 9581, 1 (190.0); LACM 9621, 1 (198.0); LACM 9704, 1 (146.6); LACM 9727, 1 (97.1); SIO63-393, 1 (161.3); SIO62-450, 1 (156.3); SIO67-104, 1 (151.8). Expressed as thousandths of the S.L. and given as the mean, and range (values in parentheses). Body, depth at dorsal origin, 119 (105-127). Caudal peduncle: least depth, 61 (55-69); length, 205 (191-225). Adipose fin: distance to midcaudal rays, 165 (154-176); length of base, 12 (8-16); length of fin, 23 (18-30). Anal fin: length of base, 155 (137-180); length of longest ray, 72 (53-94). Dorsal fin: length of base, 39 (33-43); length of longest ray, 66 (53-85); dorsal origin to anal origin (distance between verticals), 255 (238-270); end of dorsal base to base of midcaudal rays, 558 (533-577). Pectoral fin, length of longest ray, 61 (35-84). Pelvic fin, length of longest ray, 158 (133-198). Pelvic insertion to anal origin, 309 (294-330). Pectoral insertion to pelvic insertion, 146 (139-154). Anus to anal origin, 16 (11-20). Distance from snout to: anus, 646 (624-664); dorsal origin, 405 (391-428); anal origin, 660 (637-681); pectoral insertion, 212 (204-231); pelvic insertion, 360 (342-382); anterior margin of eye, 57 (49-64). Head length, 207 (194-220). Postorbital head length, 90 (81-107). Eye: horizontal diameter, 62 (52-68); vertical diameter, 57 (53-63). Interorbital width, 12 (10-16). Upper jaw length, 143 (134-152). Lower jaw length, 163 (151-172). Longest dentary tooth, 23 (19-26).

BODY: Body relatively massive, shallow. Body depth 8.84 (7.90 - 12.40) in S.L. Peduncle depth 3.60 (3.13 - 5.00) in H. L. (head length). Peduncle length 1.01 (0.88 - 1.13) in H.L.

SKIN AND SCALES: About five series of body scales from lateral line to dorsal origin, about six series from lateral line to anal origin. About 26 rows of scales from occiput to dorsal origin and about 32 rows from dorsal origin to adipose fin. Lateral line scales moderate in size, height of lateral line scales not exceeding twice the height of adjacent body scales. Lateral line scales 54-58 in 18 specimens counted. Lateral line scale above anal origin, based on 16 (95.8-203.0) specimens: H/L 1.20 (1.11-1.33); T/L .482 (.368-.540); P/L .225 (.200-.272); height of scale slightly exceeding length, tympanum provided with two anterolateral spines (fig. 16), moderately alate, completely covering moderate central pore. Lateral line scale above pectoral insertion, based on 2 (198.0-203.0) specimens and listed in that order: H/L 1.11-1.10; T/L .329-.300; P/L

.177-.187. Penultimate lateral line scale, based on 5 (95.8-203.0) specimens: H/L 1.25 (1.18-1.36); T/L .730 (.650-.802); P/L .275 (.261-.284). Ultimate lateral line scale, based on 1 (203.0) specimen, imperforate, H/L .761.

HEAD: Dorsal profile inclined steeply. Snout length exceeds horizontal eye diameter. Postorbital head depth and width subequal to body depth and width.

Eyes moderately large, directed dorsoanteriad. Pearl organ nearly elliptical, with tilt of major axis normal to visual axis of eye. Head length (H.L.) 4.84 (4.55-5.16) in S.L. Snout length 3.68 (3.44-4.03) in H.L. Horizontal eye diameter 3.34 (3.13-3.82) in H.L. Postorbital head length 2.31 (2.06-2.47) in H.L. Interorbital width 18.4 (14.0-23.6) in H.L.

Head densely pigmented on all external surfaces. Especially dense pigment at dorsoposterior corner of orbit, along dentigerous surface of premaxillary and dentary, and bordering anterior margin of eye.

Subopercle distinctly larger than opercle. Posterior border of opercle rounded. Both bones membranous. Pectoral insertion opposite a notch at dorsoposterior corner of subopercle, ventral to opercle-subopercle border.

Pseudobranchiae well-developed. Counts based on 4 (57.1, 95.8, 146.6, 198.0) specimens and listed in that order: 10, 13, 13, 12. Gill filaments moderately elongate, extending to edge of gill covers. Gill membranes united under anterior margin of orbit.

MOUTH: Upper jaw length 1.45 (1.36-1.49) in H.L. Lower jaw length 1.27 (1.19-1.32) in H.L. Upper jaw terminating at a vertical through posterior margin of orbit.

Tooth counts based on 5 (57.1, 95.8, 118.0, 146.6, 203.0) specimens and listed in that order. Premaxillary tooth counts: 42, 46, 58, 80, 166. Dentary tooth counts: lateral, 36, 34, 39, 47, 76; medial, 6, 8, 8, 9, 12. Palatine tooth counts: 7, 7, 9, 13, 12. Basihyal teeth neither hooked nor lanceolate in adults (but hooked in larvae). Basihyal tooth counts (including 1-2 small teeth over anterior terminus of first basibranchial): 9, 7, 8, 9, 12. Longest dentary tooth 9.32 (7.65-11.10) in H.L.

FINS: Dorsal moderately high, length of longest dorsal ray 6.6 (5.3-8.5) per cent S.L. Dorsal base short, 3.9 (3.3-4.3) per cent S.L. Adipose fin much reduced in adults, adipose base entirely behind a vertical through base of last anal ray. Appressed pelvic fins reaching about onehalf distance between pelvic insertion and anus. Pectorals considerably reduced in size, rays short and slender. Anal base short, 15.5 (13.7-18.0) per cent S.L. Anal origin considerably behind midlength, preanal distance 66.0 (63.7-68.1) per cent S.L.



FIG. 17. Development of *Benthalbella dentata*. A. Larva, NMFS, MT 978, 42.8. B. Metamorphic specimen, LACM 3258, 49.6. C. Metamorphic specimen, SIO63-411, 53.0. Asterisk (*) indicates position of anus.

COLOR: Color in alcohol uniformly brown. Pigment present on all areas of body and fins. Pigment outlining scale pockets expecially dense. Peritoneum with intense black pigment.

Development.—Description of development in *B. dentata* based on 89 (20.0-54.7) larvae and 7 (49.6-57.1) metamorphosing specimens. Figure 17 illustrates the development of *B. dentata*.

RECOGNITION: Larvae of *B. dentata* are distinguished by the following combination of characters: pelvic insertion considerably in advance of dorsal origin, scattered black melanophores present on pectoral fin prior to (but not after) ossification of fin rays, base of dorsal adipose fin extending behind vertical through base of last anal ray, anal 17-21, dorsal 6-8 (usually 6-7).

FINS: Smallest available specimen (20.0) barely beyond finfold stage, with caudal and a few dorsal pectoral rays ossified, but no other ossified rays present. Complete ossification of all fin rays occurs before 28-30 mm. Apparent order of ossification: caudal, dorsal pectoral rays, dorsal fin, anal, pelvics, ventralmost pectoral rays.



F1G. 18. Representation of elongation of gut at onset of metamorphosis in *B. dentata*. Ordinate and abscissa, measurements in millimeters. Circles: distance between pelvic fin insertion and anal origin. Triangles: distance between pelvic fin insertion and anus. Open symbols: larval specimens. Closed symbols: metamorphic and adolescent specimens.

METAMORPHOSIS: 3 (49.6-51.8). Initiation of metamorphosis indicated by appearance of peritoneal pigment in mesentary dorsal to gut, extending from just behind pectoral base to just behind pelvic base. Pigment not appearing as peritoneal sections but developing uniformly. Coincident with appearance of pigment is a noticeable rearward elongation of gut (fig. 18), and a simultaneous rearward expansion of the caecum. Initial pigment on head consisting of a patch of melanophores on occiput, a streak of black pigment anterior to eye, and a light patch of pigment around nostrils.

4 (52.3-57.1). Peritoneal pigment develops rapidly, and in these larger specimens peritoneal pigment already forming a complete tube around the gut. Initial peritoneal pigment expanding laterad and ventrad to form tube, as well as expanding posteriad with concomitant posteriad elongation of gut. Elongation of gut continuing until anus reaches adult position, immediately before anal origin. Concomitant with increasing gut length is continuing posteriad expansion of caecum, and first appearance of gonad. Ventral adipose completely reabsorbed in 53.0 mm. specimen, and dorsal adipose base much reduced. Head pigmentation becoming extensive, well-developed pigment on occiput, around and below orbit, on snout, lower jaw, and within oral cavity. Body pigmentation appears on





caudal peduncle in close association with presumptive lateral line scale pockets. Lateral line scale pockets clearly visible in 57.1 mm. specimen.

Completion of metamorphosis coincident with point of maximum rearward expansion of gut. A 68.3 mm. adolescent specimen in my material is essentially adult in all characters.

Distribution.— B. dentata is limited to the North Pacific. All but seven specimens are from east of 150° 10' W, and have been taken from the Gulf of Alaska (57° 46' N) to off Guadalupe Island, Mexico (29° 12.1-13.8' N). Figure 19 illustrates the distribution of B. dentata.

Larvae of *B. dentata* have been taken in each of the 12 months of the year, with no apparent peaks in abundance or seasonality in occurrence of different size classes.

A vast majority of all specimens of *B. dentata* were taken in hauls to between 500-1000 m. On only three occasions have adults been taken in hauls to less than 500 m., twice by night (both 0-450 m.), and once by day (0-450 m.). Most larvae were likewise taken in hauls to depths greater than 500 m., but a number of larvae were taken in hauls, both day and night, to lesser depths. Larvae of *B. dentata* have never been taken, however, in hauls to less than 150 m., suggesting that the larvae of this species do not occur as shallowly as those of *B. linguidens* (see below).

Material examined.—A total of 120 (20.0-203.0) specimens from 102 collections. LACM: LACM 3258, 1 (49.6); LACM 6724, 4 (31.5-37.0); LACM 6882, 1 (26.0); LACM 7530. 1 (25.1); LACM 8992, 1 (40.1); LACM 8996, 1 (31.5); LACM 9033, 3 (21.2-27.7); LACM 9034, 2 (22.0-24.9); LACM 9037, 2 (27.2-33.8); LACM 9038, 1 (37.0); LACM 9065, 1 (32.3); LACM 9253, 2 (23.3-95.8); LACM 9364, 1 (191.5); LACM 9365, 1 (163.1); LACM 9373, 1 (46.0); LACM 9374, 1 (37.7); LACM 9494, 1 (44.0); LACM 9499, 1 (34.0); LACM 9567, 1 (187.0); LACM 9568, 1 (54.5); LACM 9581, 1 (190.0); LACM 9582, 1 (41.0); LACM 9586, 1 (39.9); LACM 9617, 1 (36.0); LACM 9621, 1 (198.0); LACM 9622, 1 (38.8); LACM 9627, 2 (34.2-37.5); LACM 9640, 1 (35.3); LACM 9645, 1 (29.6); LACM 9679, 1 (20.0); LACM 9704, 1 (146.6); LACM 9713, 1 (51.8); LACM 9726, 1 (24.7); LACM 9727, 1 (97.1); LACM 9734, 1 (57.1); LACM 9760, 1 (36.2); LACM 9838, 1 (35.5); LACM 9840, 3 (37.1-41.0); LACM 9841, 1 (37.5); LACM 9842, 1 (39.6); LACM 9843, 1 (32.4); LACM 9845, 4 (28.6-47.6); LACM 9849, 1 (25.8); LACM 9864, 1 (23.2); LACM 9951, 1 (52.3); LACM 9952, 1 (27.4); LACM 9975, 1 (31.2); LACM 9988, 1 (41.0); LACM 30120. 1 (39.9); LACM 30188, 2 (25.5-28.1); LACM 30200, 1 (20.4). NMFS: material deposited in larval fish collection of Dr. E. H. Ahlstrom, Fishery-Oceanography Center, La Jolla, California. BB 199-276, 2 (37.5-38.5); BB 199-285, 1 (29.0); BB 199-287, 1 (30.4); BB 199-290. 1 (38.1); BB 199-291, 1 (29.7); BB 202-40, 1 (38.6); BB 202-53, 1 (38.5); MPS 933, 1 (42.0); MT 152, 1 (51.8); MT 593, 1 (42.5); MT 594, 1 (40.0); MT 682, 1 (50.5); MT 954, 1 (34.1); MT 978, 1 (42.8); MT 1010, 1 (46.5); YAQUINA 6505, 2 (54.7-68.3); YAQUINA 6507, 1 (34.0). SIO: S1O51-354, 1 (51.0); S1O51-361, 1 (62.5); S1O51-362, 1 (187.0); S1O51-363, 1 (118.0); \$1053-340, 1 (56.5); \$1056-114, 1 (33.1); \$1060-287, 1 (144.6); \$1063-379, 1 (115.0); S1O63-308, 1 (183.0); S1O63-393, 1 (161.3); S1O63-400, 1 (41.4); S1O63-411, 2 (30.4-53.0); S1O63-450, 1 (156.3); S1O64-1028, 1 (41.0); S1O65-445, 1 (26.9); S1O65-556, 1 (31.0); S1O66-53, 1 (46.8); S1O66-440, 1 (22.9); S1O66-536, 1 (31.0); S1O66-541, 1 (31.0);

S1066-549, 1 (37.5); S1066-553, 1 (34.9); S1067-104, 2 (46.1-151.8); S1067-112, 1 (37.4); S1067-113, 1 (48.2); S1067-116, 1 (41.5); S1067-122, 1 (48.3); S1070-19, 1 (203.0); S1071-15, 1 (148.0). USC: USC-V 10541, 1 (189.0). USNM: USNM 108145, 1 (162) holotype; USNM uncat. H6204, 60.60, 1 (58.5).



FIG. 20. Benthalbella elongata (Norman). A. Adult, 187 mm. (after Andriashev, 1960, p. 564).
B. Larva, USC-E 2205, 51.4. C. Lateral line scale above analorigin, USC-E 1036, 200.0.
D. Lateral line scale above pectoral insertion, USC-E 1064, 200.0.
E. Penultimate lateral line scale, USC-E 1050, 181.7.

Benthalbella elongata (Norman) 1937. Figure 20.

Scopelarchus elongatus Norman 1937, p. 86; Mead and Böhlke, 1953, p. 244. Neoscopelarchoides elongatus: Marshall, 1955, p. 310; Andriashev, 1960, p. 563; Mc-Allister, 1968, p. 95. Benthalbella elongata: Bussing and Bussing, 1966, p. 58. Benthalbella elongatus: Rofen, 1966, p. 573.

Holotype-198 mm. S.L. BANZ Antarctic Research Expedition,

station 67. Southern Indian Ocean, 45° 53' S, 84° 33' E. (2 m. ring net: 2000 mwo), March 7, 1930. Holotype deposited at British Museum (Natural History).

Comparative diagnosis—A species of Benthalbella with 9-10 dorsal rays, 24-28 anal rays, 19-23 pectoral rays, and 61-65 lateral line scales. Peritoneal pigment present in all post-metamorphic specimens (cf. Bussing and Bussing, 1966, p. 59) but consisting of scattered small melanophores, not uniformly black or brown. The combination of these characters distinguishes *B. elongata* from all other known scopelarchid species.

Description—Based on 18 (33.0-84.2) larvae, 10 (89.1-102.3) metamorphosing specimens, and 40 (98.6-234.0) adolescents and adults. With the exception of meristic characters, the description given first is that based on adults, followed by an account of development.

MERISTIC CHARACTERS: Values for the holotype (from Marshall, 1955, p. 310), given in parentheses. Dorsal 9-10 (9); anal 24-28 (26); pectoral 19-23 (22); lateral line scales 61-65 (62); vertebrae 62-65 (61). Marshall (1955) reported eight dorsal rays in one of his two *Discovery* specimens.

PROPORTIONAL DIMENSIONS: Based on 10 (98.6-223.0) specimens: ISH 1684, 1 (220.0); USC-E 109, 1 (113.0); USC-E 313, 1 (115.3); USC-E 802, 1 (139.1); USC-E 866, 1 (107.4); USC-E 1050, 1 (181 7); USC-E 1064, 1 (200.0); USC-E 1580, 1 (147.6); USC-E 1615, 1 (223.0); USC-E 2174, 1 (98.6). Expressed as thousandths of the S.L. and given as the mean, range (values in parentheses), and values for the holotype (taken from Marshall, 1955, p. 310).

Body, depth at dorsal origin, 129 (101-185) 141. Caudal peduncle: least depth, 69 (55-82) 71; length, 134 (125-142) 126. Adipose fin: distance to midcaudal rays, 161 (152-172); length of base, 65 (43-97); length of fin, 64 (51-74). Anal fin: length of base, 227 (200-254); length of longest ray, 89 (74-103). Dorsal fin: length of base, 62 (54-66); length of longest ray, 89 (65-113); dorsal origin to anal origin (distance between verticals), 241 (221-262); end of dorsal base to base of midcaudal rays, 532 (519-547). Pectoral fin, length of longest ray, 99 (84-117). Pelvic fin, length of longest ray, 128 (110-140). Pelvic insertion to anal origin, 275 (256-288). Pectoral insertion to pelvic insertion, 162 (140-184). Anus to anal origin, 26 (22-35). Distance from snout to: anus, 642 (618-673); dorsal origin, 419 (393-437) 391; anal origin, 662 (640-691) 646; pectoral insertion, 236 (202-268) 217; pelvic insertion, 398 (374-431) 379; anterior margin of eye, 79 (66-93) 61. Head length, 221 (195-237) 198. Postorbital head length, 80 (71-87). Eye: horizontal diameter, 63 (50-72) 56; vertical diameter, 59 (50-66). Interorbital width, 19 (16-21) 16. Upper jaw length,

165 (144-180). Lower jaw length, 194 (169-212). Longest dentary tooth, 32 (24-41).

BODY: Body shallow, moderately compressed. Body depth 8.00 (5.42-9.95) in S.L. Peduncle depth 3.30 (2.47-4.15) in head length (H.L.). Peduncle length 1.65 (1.38-1.82) in H.L.

SKIN AND SCALES: Body scales moderate in size 9-10 rows from lateral line to dorsal origin, 9-10 rows from lateral line to anal origin, ca. 29 rows from occiput to dorsal origin, ca. 53 rows from dorsal origin to adipose fin. Lateral line scales relatively small, less than twice as deep as adjacent body scales. Lateral line scales numbering 61-65 in 24 specimens counted. Lateral line scale above anal origin, based on 12 (102.5-200.0) specimens: H/L, .828 (.761-.906); T/L, .359 (.213-.494); P/L, .279 (.212-.367); height of scale less than length, tympanum with two spikelike projections at anterolateral margin and moderately alate posteriorly, tympanum completely covering moderately large central pore. Lateral line scale above pectoral insertion, based on 7 (107.4-223.0) specimens: H/L .794 (.650-.902); T/L .314 (.211-.439); P/L .228 (.195-.298); tympanum poorly developed, in smaller specimens tympanum height less than or equal to pore height. Penultimate lateral line scale based on 4 (181.7, 186.0, 200.0, 223.0) specimens and listed in that order: H/L 1.02, 1.08, .952, 1.12; T/L .476, .538, .525, .548; P/L .257, .253, .248, .258. Ultimate lateral line scale missing in all specimens examined, due to damage.

HEAD: Dorsal profile horizontal posterior to mid-interorbital region, moderately descending to snout anterior to mid-interorbital region. Postorbital head depth and width subequal to body depth and width. Eyes relatively small, tilted slightly forward. Head length 4.54 (4.23-5.13) in S.L. Snout length 2.80 (2.50-2.98) in H.L. Horizontal eye diameter 3.55 (3.10-3.92) in H.L. Postorbital head length 2.78 (2.43-3.24) in H.L. Interorbital width 11.8 (10.5-13.8) in H.L.

Head densely pigmented on all external surfaces, with pigment present on branchiostegal membranes and within oral and branchial cavities. Pigment lining dorsal margin of orbit, snout, and bordering dentigerous areas of jaws, especially dense.

Subopercle larger than opercle, both bones plow-share shaped, rounded, nonserrate. Pectoral insertion opposite a moderate indentation in dorsoposterior margin of subopercle.

Pseudobranchiae well-developed. Counts based on 3 (102.5, 117.9, 200.0) specimens and listed in that order: 15, 13, 16. Gill filaments relatively short, not reaching posterior border of gill covers. Gill membranes united under middle of eye.

MOUTH: Upper jaw length 1.34 (1.30-1.39) in H.L. Lower jaw length 1.14 (1.10-1.18) in H.L. Upper jaw terminating slightly behind a vertical through posterior margin of orbit.

Tooth counts based on 4 (102.5, 117.9, 126.1, 200.0) specimens and listed in that order. Premaxillary tooth counts: 33, 73, 70, 70. Dentary tooth counts: lateral, 28, 39, 37, 46; medial, 8, 10, 11, 11. Palatine tooth counts: 11, 13, 12, 13. Vomerine teeth small, one per side (two on one side in one specimen). Lingual teeth restricted to basihyal (except 1-2 small teeth over anterior terminus of basibranchial tooth-plate). Lingual tooth counts: 8, 10, 11, 7. Basihyal teeth hooked and lanceolate in smaller specimens, decreasing in size but more strongly hooked posteriorly; basihyal teeth essentially straight and unhooked in larger specimens. Longest dentary tooth 7.16 (5.75-8.60) in H.L.

FINS: Dorsal moderately high, longest dorsal ray 8.9 (6.5-11.3) per cent S.L. Dorsal base moderate, length of base 6.2 (5.4-6.6) per cent S.L. Adipose moderately sized, anterior margin indistinct, continuous with a low, scaly, fatty ridge extending to over anterior anal rays. Appressed pelvic rays reaching one-third to one-half distance between pelvic insertion and anus. Appressed pectoral rays reaching about one-half distance from pectoral insertion to pelvic insertion. Anal base moderate, 22.7 (20.0-25.4) in S.L. Anal origin well behind midlength, preanal distance 66.2 (64.0-69.1) per cent S.L.

COLOR: Color in alcohol a uniform dull brown with edges of scale pockets slightly emphasized by heavier pigmentation. Pigment present on all fins. Peritoneal pigment sparse, even in largest adults, consisting of scattered small melanophores producing a "dusty" appearance of the peritoneum, not approaching the uniform brown or black peritoneal pigment found in all other scopelarchid species.

Development.—The description of development in *B. elongata* is based on 18 (33.0-84.2) larvae and 10 (89.1-102.3) metamorphosing specimens. A larval *B. elongata* is illustrated in Figure 20.

RECOGNITION: Pre-metamorphic specimens of *B. elongata* are distinguished by the following combination of characters: pelvic insertion well in advance of dorsal origin, pigment (other than eye) lacking, dorsal 9-10, anal 24-28, pectoral 19-23.

FINS: In the smallest available specimen (33.0) all fins except ventral half of pectoral, pelvics, and procurrent caudal rays, formed if not fully ossified. Dorsal adipose extending anteriorly to a vertical over one-half the pelvic-anal distance. Ventral adipose large, reaching from anus (just behind pelvic base) to anal origin. Apparent order of fin ray ossification: caudal, dorsalmost pectoral rays, dorsal, anal, pelvics, ventralmost pectoral rays.

GUT: Post-pelvic gut length short in larvae but reaching to just before anal origin during metamorphosis. Caecum readily visible in larvae as short blind sac not reaching posteriorly as far as pelvic insertion, even in largest (84.2) larva, but rapidly increasing in length during metamorphosis, reaching to just before anus in adolescents and adults.

METAMORPHOSIS: 5 (89.1-95.4). Onset of metamorphosis indicated by strips of paired peritoneal pigment dorsolateral to gut, not forming distinct peritoneal sections, and extending from anterior end of abdominal cavity to one-third pelvic-anus distance behind pelvic bases. Caecum expanding posteriad, reaching slightly beyond maximum posterior



FIG. 21. Distribution of *Benthalbella elongata* (Norman). Open symbols: records based solely on larvae. Closed symbols: records based on adults and metamorphosing specimens.

extension of peritoneal pigment. Investiture of abdominal wall by muscle tissue beginning. Head and body pigmentation beginning to appear, as patches of fine melanophores over much of head and body, especially evident at bases of medial fins, along lateral line, on ventral body wall anterior to anal base, around orbit, lining upper and lower jaws, and on brenchiostegal membranes.

5 (92.6-102.3). In larger metamorphosing specimens, two thin strips of peritoneal pigment expand and coalesce dorsally, forming a roof of pigment above gut, but failing to meet midventrally during metamorphosis. These larger specimens have the head and body nearly covered with uniform pigmentation, have the abdominal body wall completely invested with muscle tissue, and exhibit maximum posteriad expansion of gut and caecum.

1 (98.6). This, the smallest adolescent specimen available to me, is essentially identical to the larger adults in pigmentation and morphology.

Distribution.—Benthalbella elongata is an Antarctic species known only from south of the Subtropical Convergence. The northernmost record for this species is 39° 19' S, 48° 02' W, in the South Atlantic; the southernmost record is 66° 08' - 65° 51' S, 82° 32' - 28' W, in the South Pacific (fig. 21).

Larvae have been captured in January, February, June, September, November, and December, with no apparent peaks in abundance or differences between size classes. Almost all hauls successfully capturing *B. elongata* were to depths in excess of 500 m. Larvae have been taken in the upper 200 m.; adults on four occasions in the upper 400 m., but have not been taken in hauls shallower than 200 m.

Material examined.—A total of 68 (33.0-234.0) specimens from 48 collections. **ISH:** ISH 557/71, 1 (227); ISH 631/71, 1 (91.6); ISH 730/71, 1 (220); ISH 803/71, 2 (220-222); ISH 920/71, 1 (229.5); ISH 1049/71, 4 (203-234); ISH 1684, 1 (220.0); ISH uncat. WH 363 111/71, 1 (89.1). **SIO:** SIO61-41 (84.2). SIO61-43, 1 (100.3). **SOSC:** (all station numbers given are *Eltanin* field numbers) E 2025, 1 (102.5); E 2253, 1 (46.4); E 2263, 1 (137.5); E 2269, 1 (40.6); E 2288, 9 (41.4 - 58.5); E 2301, 1 (53.9); **USC:** (all station numbers given are *Eltanin* field numbers) E 109, 4 (92.0-113.0); E 148, 1 (117.9); E 313, 2 (100.1-115.4); E 379, 1 (66.5); E 388, 1 (155.1); E 802, 1 (139.1); E 866. 1 (107.4); E 992, 1 (ca. 100); E 1036, 2 (186.0 - 200.0); E 1050, 1 (181.7); E 1064, 1 (200.0); E 1107, 1 (101.5); E 1179, 1 (ca. 108); E 1290, 1 (97.6); E 1307, 1 (121.8); E 1323, 1 (99.8); E 1337, 1 (68.6); E 1364, 1 (196.5); E 1380, 1 (92.6); E 1389, 1 (106.8); E 1392, 2 (117.9-126.1); E 1454, 1 (95.4); E 1580, 1 (147.6); E 1607, 1 (93.9); E 1615, 1 (223.0); E 1637, 1 (135.3); E 1676, 1 (124.2); E 1982, 1 (33.0); E 2174, 1 (98.6); E 2205, 1 (51.4); E 2216, 2 (45.8-102.3); E 2244, 2 (100.6-113.8).

Benthalbella infans Zugmayer 1911. Figure 22.

Benthalbella infans Zugmayer 1911a, p. 14; 1911b, pp. 140-142; Schmidt, 1918, p. 34; Parr, 1928, p. 157; 1930, p. 156; Nybelin, 1948, pp. 44-48; Mead and Böhlke, 1953,



FIG. 22. *Benthalbella infans* Zugmayer. A. Adult. Discovery station 1759, 138 mm. (Holotype of *Neoscopelarchoides dubius* Marshall 1955, adapted from Marshall, 1955, p. 309). B. Lateral line scale above anal origin, DANA 3624 1, 132.1. C. Lateral line scale above pectoral insertion, DANA 3624 1, 132.1. D. Penultimate lateral line scale, UH 70/9/14, 113.3.

p. 244; Koefoed, 1955, p. 7; Rass, 1955, pp. 329-330; Bussing and Bussing, 1966, p. 59; Rofen, 1966e, p. 573; Backus *et al.*, 1969, p. 94. Merrett, Badcock, and Herring, 1973, pp. 1-48.

Benthalbella dubius: Rofen, 1966e, p. 573.

Neoscopelarchoides dubius Marshall, 1955, pp. 309-310; Backus et al., 1965, p. 145. Neoscopelarchoides sp. Marshall, 1955, pp. 311-312.

?Neoscopelarchoides sp. A.: Backus et al., 1965, p. 145.

Omosudis lowei (in part, nec Guenther, 1887): Roule, 1928, pp. 6-9; Roule and Angel, 1930, p. 57. misidentification.

Scopelarchus guentheri (in part): Craddock and Mead, 1970, p. 3.26. misidentification

Murray and Hjort (1912, p. 746) reported "a new fish resembling *Dysomma* (sic)," captured in the North Atlantic by the *Michael Sars* Expedition. Although the authors provided a figure of this fish, they did not describe it. Koefoed (1955, plate 1, fig. A) recognized the specimen of Murray and Hjort to be *B. infans*, and republished their figure. Merrett et al. (1973) have discussed reproduction, development, and aspects of the biology of this species.

Holotype.—54 mm. S.L., Princess Alice 3036. Eastern North Atlantic, 36° 07' N, 10° 18' W, 7 September, 1910.

Comparative diagnosis.—A species of *Benthalbella* with 8-9 dorsal rays (49 of 50 specimens had dorsal = 9); 20-25 anal rays; 25-28 pectoral rays; 55-59 lateral line scales; luminous organs (IO, POa, POp, AO, see above) present, with dense black band of pigment between POp and AO.

The combination of these characters distinguishes *B. infans* from all other known scopelarchids.

Description.—Based on 73 (6.6-77.5) larvae, 5 (55.1-76.0) metamorphosing specimens, and 8 (85.8-137.4) adults. With the exception of meristic characters, the description given first is that of adults, followed by an account of development.

MERISTIC CHARACTERS: Values listed in parentheses are from three specimens: 1 (54) holotype of *B. infans* (taken from Zugmayer, 1911b, pp. 140-142); 1 (138) holotype of *Neoscopelarchoides dubius* Marshall (taken from Marshall, 1955, pp. 308-311); 1 (60.5) specimen listed as *Neoscopelarchoides* sp. (Marshall, 1955, pp. 309-311; counts given are those of Marshall); and are listed in that order: dorsal 8-9 (9, 9, 9); anal 20-25 (17, 21, 22); pectoral 25-28 (22, 27, 24); lateral line scales 55-59 (-, 59, -); vertebrae 55-58 (-, 57, -). Zugmayer's counts for the anal, pectoral, and pelvic fins are too low for this species, and are no doubt related to the difficulties involved with obtaining counts from larval material.

PROPORTIONAL DIMENSIONS: Based on 2 (66.3-76.0) metamorphosing specimens and 6 (95.1-137.4) adults: DANA 1247 I, 1 (66.3); DANA 3624 I, 1 (132.1); DANA 3751 I, 1 (95.1); ISH 329, 1 (76.0); ISH 1437, 1 (137.4); UH 70/9/14, 1 (113.3); UH 70/9/15, 1 (95.6); USC - E 1769, 1 (121.5), from all three oceans. Expressed as thousandths of the S.L. and given as the mean, range (values in parentheses), and values for the holotype of Neoscopelarchoides dubius Marshall (138 mm., southern Indian Ocean, 31° 54.5' S, 51° 27.9' E, proportions taken from Marshall, 1955, pp. 309-310). Body, depth at dorsal origin, 126 (82-167) 175. Caudal peduncle; least depth, 60 (46-67) 62; length, 127 (115-132) 112. Adipose fin: distance to midcaudal rays, 167 (153-181); length of base, 63 (37-84); length of fin, 52 (34-68). Anal fin: length of base, 202 (191-213); length of longest ray, 78 (67-90). Dorsal fin: length of base, 58 (53-62); length of longest ray, 83 (63-113); dorsal origin to anal origin (distance between verticals). 274 (263-298); end of dorsal base to base of midcaudal rays, 533 (514-552). Pectoral fin, length of longest ray, 146 (116-186) 210. Pelvic fin, length of longest ray, 207 (151-267) 290. Pelvic insertion to anal origin, 306 (287-330). Pectoral insertion to pelvic insertion, 162 (145-179). Anus to anal origin (based on adults only), 47 (27-61). Distance from snout to: anus (based on adults only), 620 (546-679); dorsal origin, 415 (388-450) 384; anal origin, 693 (662-724) 615; pectoral insertion, 244 (221-261) 255; pelvic insertion, 402 (389-420) 409; anterior margin of eye, 81 (74-90) 87. Head length, 220 (211-230) 228. Postorbital head length, 67 (54-74). Eve: horizontal diameter, 71 (62-83) 58; vertical

diameter, 67 (53-79). Interorbital width, 14 (11-21) 7. Upper jaw length, 164 (156-171) 152. Lower jaw length, 188 (175-196) 203. Longest dentary tooth, 33 (29-41).

BODY: Body shallow, moderately compressed. Body depth 8.27 (6.00-12.25) in S.L. Peduncle depth 3.74 (3.40-4.85) in head length (H.L.). Peduncle length 1.73 (1.61-1.84) in H.L.

SKIN AND SCALES: Body scales moderate in size, 8-9 rows from lateral line to dorsal origin, 10-11 rows from lateral line to anal origin, longitudinal rows not countable due to damage in all specimens. Lateral line scales relatively small, less than twice as deep as adjacent body scales. numbering 55-59 in eight specimens counted. Lateral line scale above anal origin based on five (95.1-132.1) specimens: H/L .874 (.761-.942); T/L .534 (.448-.588); P/L .241 (.209-.265); height of scale less than length, anterior tympanum margin more or less truncate, tympanum moderately alate posteriorly, completely covering central pore. Marshall (1955, p. 309, text-fig. 2) illustrated a lateral line scale taken from the holotype of Neoscopelarchoides dubius, without indicating the position along the lateral line the scale was taken from. The dimensions of this scale (taken from the figure) are as follows: H/L .851; T/L .300; P/L .163. Lateral line scale above pectoral insertion based on 2 (121.5-132.1) specimens and listed in that order: H/L .800, .722; T/L .356, .348; P/L .198, .160. Penultimate lateral line scale, based on 1 (113.3) specimen: H/L 1.12; T/L .626; P/L .288. Ultimate lateral line scale missing from all specimens examined due to damage.

HEAD: Dorsal profile descending at slight angle to snout. Eye diameter less than snout length. Head depth and width subequal to body depth and width. Eyes relatively small, directed straight upward or tilted slightly forward. Head length 4.56 (4.35-4.75) in S.L. Snout length 2.74 (2.42-3.06) in H.L. Horizontal eye diameter 3.10 (2.70-3.42) in H.L. Postorbital head length 3.31 (3.02-4.15) in H.L. Interorbital width 16.20 (10.36 -19.33) in H.L.

Head densely pigmented on all external surfaces with pigment on branchiostegal membranes and inside branchial cavity. Little or no pigment within oral cavity. Especially dense pigment on occiput, around orbit, on interorbital and snout, and bordering dentigerous areas of jaws.

Subopercle larger than opercle, both plowshare shaped, with rounded, nonserrate posterior margins. Pectoral insertion opposite a rounded notch in dorsoposterior margin of subopercle.

Pseudobranchiae well-developed, counts based on 3 (95.1, 95.6, 132.1) specimens and listed in that order: 13, 15, 15. Gill filaments relatively

short, not reaching posterior border of gill covers. Gill membranes united under midorbit.

MOUTH: Upper jaw length 1.34 (1.31-1.39) in H.L. Lower jaw length 1.17 (1.12-1.25) in H.L. Upper jaw terminating at a point slightly anterior to posterior margin of orbit.

Tooth counts based on 6 (60.5, 77.5, 95.1, 95.6, 132.1, 138) specimens and listed in that order (counts of 60.5 and 138 mm. specimens taken from Marshall, 1955, p. 311). Premaxillary tooth counts: 30, 52, 58, 57, 77, 80. Dentary tooth counts: lateral, 20, 23, 29, 30, 31, 30; medial, 7, 11, 9. 6, 10, 9. Palatine tooth counts: 12, 11, 11, 12, 9, 11. Lingual tooth counts: 7, 10, 13, 11, 12, 14. Basihyal teeth hooked and lanceolate in smaller specimens, decreasing in length but more hooked posteriorly. Basihyal teeth nearly straight and unhooked at least anteriorly in larger adults. Longest dentary tooth 6.77 (5.23-7.72) in H.L.

FINS: Dorsal moderately long, length of longest dorsal ray 8.3 (6.3-11.3) per cent S.L.; dorsal base moderate, 5.8 (5.3-6.2) per cent S.L. Adipose with densely pigmented base. Adipose margin merging indistinctly with low fatty scaly middorsal ridge extending anteriorly to over middle of anal fin base. Appressed pelvics reaching anus, appressed pectorals reaching slightly beyond pelvic insertion. Anal base moderate, length of base 20.2 (19.1-21.3) per cent S.L. Anal origin well behind midlength, preanal distance 69.3 (66.2-72.4) per cent S.L.

COLOR: Color in alcohol a uniform dull brown with edges of scale pockets emphasized by slightly heavier pigmentation. Pigment present on all fins. A dense black stripe of pigment on midventral contour between POp and AO luminous organs. Peritoneum dense black.

Development.—The description of development in *B. infans* is based on 65 (6.6-77.5) larvae and 5 (55.1-76.0) metamorphosing specimens. Figure 23 illustrates development in this species.

RECOGNITION: Premetamorphic specimens of *B. infans* are distinguished by the following combination of characters: dorsal 8-9 (usually 9), anal 20-25, pectoral 25-28; pelvic insertion well in advance of dorsal origin, no pigment (other than eyes) prior to metamorphosis.

FINS: Smallest specimens (6.6-10.5) in fin-fold stage with no ossified rays. Fin ray ossification complete by 30-35 mm. Apparent order of ossification: caudal, dorsalmost pectoral rays, dorsal, anal, pelvic, ventralmost pectoral rays. In largest (77.5) larval specimen dorsal adipose extending to a vertical through two-thirds the pelvic-anal distance behind the pelvic insertion, while ventral adipose fin occupies four-fifths of the pelvic-anal distance anterior to the anal origin.





METAMORPHOSIS: 5 (55.1-76.0) Peritoneal pigment appearing as single dorsomedial thin strip of pigment, not as an organized peritoneal section, extending in 55.1 mm. specimen from medial to pectoral base to about one-third the distance between pectoral and pelvic insertions. Peritoneal pigment apparently rapidly expanding laterad and posteriad, forming a tube around the gut. Head and body pigment appearing at same time as peritoneal pigment, with dense areas on cranium, snout, orbit, jaws, and body above lateral line. Caecum expanding rapidly posteriad but not reaching adult position, just anterior to anus, until after completion of metamorphosis.

3 (85.8, 95.1, 95.6) These, the youngest adolescent specimens available to me, are essentially identical to the larger adults in pigmentation and morphology.

Discussion.—Throughout its wide range *B infans* shows little veriability with regard to meristic or morphometric characters, or larval morphology. There exists some apparent variability in size at which metamorphosis takes place, the smallest metamorphosing specimen, 55.1 mm., is from the western North Atlantic, the largest, 76.0, from the eastern North Atlantic. Intermediate in size are specimens from the western North Atlantic, 1 (66.3); eastern North Atlantic, 1 (58.5); and Indian Ocean, 1 (68.5). The Atlantic specimens were all taken in February, the Indian Ocean specimen in October.

Specimens of this species from the central North Pacific appear to have a higher number of anal rays (table 6) but do not differ in other respects. More specimens are needed from the North Pacific to determine if a difference in fact exists.

Anal fin rays	20	21	22	23	24	25	N
North Atlantic + Caribbean	2	6	2	_	1	2	13
South Atlantic, Indian, Western, Equatorial and South Pacific, including South China Sea	4	9	7	3	5	1	29
Central North Pacific including Philippine Sea	-	_	_	2	1	5	8

 TABLE 6. Geographically based comparison of anal fin ray counts in Benthalbella infans.

Distribution.—B. infans is a nearly cosmopolitan warm-water species (fig. 24) inhabiting the central and equatorial water masses of all three oceans, but not known to occur in the transition regions of the eastern Pacific, nor east of 152° W in Pacific Equatorial water. B. infans is known from both sides of the North Atlantic as well as from the Carib-





bean (but is not yet known from the Gulf of Mexico). This species, along with *Scopelarchus guentheri* (see below), appears to be the most widely ranging of all scopelarchid species.

R infans is also apparently a deep-living species. Larvae have not been taken in hauls to less than 300 m., most were taken in hauls to between 300-600 m. Larvae of *B. infans* have been taken in all parts of the oceans at all times of year. Adults have not been taken in hauls to less than 500 m., and most were taken in hauls to depths a good deal deeper than this. *B. infans* is one of the few scopelarchids known to have been captured by closing gear. Nybelin (1948, p. 44) reported 1 (84) specimen from a 2 m. ring net fished and closed at 1500 mwo, ca. 650 m., from the North Atlantic. The holotype of *Neoscopelarchoides dubius* (138 mm.) was taken in a 450 cm. closing net hauled obliquely between 1800-1100 m. in the Indian Ocean (Marshall, 1955, p. 309).

Material examined.-A total of 86 (6.6-137.4) specimens from 57 collections.

North Atlantic Ocean. DANA D1185 X1, 1 (46.4); D1189 111, 1 (52.6); D1242 V1, 1 (55.1); D1247 I, 1 (66.3); D4008 II, 1 (22.5); D4009 IX, 1 (20.0); D4009 X1, 11 (10.4-20.0); D4010 II. 1 (16.6); D4014 III, 11 (13.0-20.5); D4017 II, 2 (6.6-10.5); D4019 IV, 1 (22.0); D4019 V, 4 (13.0-25.6); D4147 VI, 1 (36.0); D4147 VII, 3 (22.5-38.8); D4149 II, 1 (39.2); D4149 II. 1 (33.1); THOR 66, 1 (53.0); THOR 91, 1 (65.0). ISH: ISH 329, 1 (76.0); ISH 430, 1 (58.5); ISH 2835/71, 1 (123.1). WHOI: RHB 1108, 1 (30.9); RHB 1275, 1 (36.1).

South Atlantic Ocean. DANA: D3996 IV, 2 (36.6-37.8). ISH 1437, 1 (137.4).

Indian Ocean. DANA D3804 1, 1 (77.5); D3804 11, 1 (17.5); D3975 1, 1 (ca. 70). S10: S1069-27, 1 (68.5); S1071-25, 1 (50.5). SOSC: TV 4-143, 1 (66.8); TV 4-147, 2 (65.2-68.5); USNM: AB 3-9, 1 (ca. 48); AB 3-10, 1 (70.6); AB 3-21, 1 (50.1); AB 3-7041, 1 (85.8); AB 6-337B, 1 (44.5); AB 6-348 A, 1 (44.5); AB 6-351C + 352A, 1 (44.9).

South China Sea. SIO: S1O70-341, 1 (70.5); S1O70-347, 1 (34.9).

Western Equatorial Pacific. DANA: D3751 1, 1 (95.1).

Central equatorial and South Pacific. DANA: D3624 1, 1 (132.1). ORSTOM: 18 [11/68, 1 (75.8); 15/8/69, 2 (56.6-60.6). S1O: S1O69-334, 1 (61.0); S1O69-342, 1 (52.0). USC: USC - E 1769, 1 (121.5). WHOI: AB X111 - 26, 1 (31.6).

Central North Pacific. SIO: S1060 - 275, 1 (34.4); S1068-495, 1 (47.0); S1070-306, 1 (48.0); S1070-309, 1 (49.3); S1070-334, 1 (52.8). **UH:** 69/11/10, 1 (57.5); 70/9/14, 1 (113.3); 70/9/15, 1 (95.6).

Benthalbella linguidens (Mead and Böhlke) 1953. Figure 25.

Scopelarchus linguidens Mead and Böhlke, 1953, pp. 241-245.

Benthalbella diaphana Rass, 1955, pp. 329-330; Bussing and Bussing, 1966, p. 59. Neoscopelarchoides linguidens: Marshall, 1955, pp. 310, 314.

Benthalbella linguidens: Rofen, 1966e, p. 573; Bussing and Bussing, 1966, p. 59.

Holotype.-USNM 163281, 47.3 mm. S.L. 45 miles east of Ohakosaki, lwate Prefecture, Japan; 39° 21' N, 142° 57.5' E, (IKMT: taken at less than 13 m.) May 26, 1952.

Comparative diagnosis.—A species of Benthalbella with 8-9 dorsal rays, 28-30 anal rays, 24-27 pectoral rays, and 66 (1 specimen) lateral



FIG. 25. *Benthalbella linguidens* (Mead and Böhlke). A. Adult. OSU 568, 221.0. B. Larva, S1063-340, 49.0. C-E. Lateral line scales from single known adult specimen, OSU 568, 221.0: C. Lateral line scale above anal origin; D. Lateral line scale above pectoral insertion; E. Penultimate lateral line scale.

line scales. The combination of these characters distinguishes *B. lin*guidens from all other known scopelarchids.

Description.—Based on 8 (48.0-85.5) larvae and 1 (221.0) adult. Description of single adult given first (except meristic characters) followed by description of larvae.

MERISTIC CHARACTERS: Given as range of values exhibited in my material and range of values for five previously reported specimens (in parentheses, all larvae, values taken from Mead and Böhlke (1953) and Rass (1955)). Dorsal 8-9 (7-10); anal 28-30 (28-30); pectoral 24-25 (24-27); lateral line scales 66 (1 specimen); vertebrae 64 (1 specimen).

PROPORTIONAL DIMENSIONS: Based on 1 (221.0) specimen, OSU 568. Expressed as thousandths of the S.L. Body, depth at dorsal origin, 149. Caudal peduncle: least depth, 72; length, 163. Adipose fin: distance to midcaudal rays, 172; length of base, 30; length of fin, 61. Anal fin: length of base, 247; length of longest ray, 86. Dorsal fin: length of base, 49; length of longest ray, 106; dorsal origin to anal origin (distance between verticals), 195; end of dorsal base to base of midcaudal rays, 537. Pectoral fin, length of longest ray, 113. Pelvic fin, length of longest ray, 136. Pelvic insertion to anal origin, 279. Pectoral insertion to pelvic insertion, 169. Anus to anal origin, 36. Distance from snout to: anus, 597; dorsal origin, 380; anal origin, 628; pectoral insertion, 219; pelvic insertion, 369; anterior margin of eye, 57. Head length, 173. Postorbital head length, 75. Interorbital width, 15. Eye: horizontal diameter, 43; vertical diameter, 48. Upper jaw length, 124. Lower jaw length, 140. Length of longest dentary tooth, 20.

BODY: Body deep, relatively massive. Body depth 6.70 in S.L. Peduncle depth 2.38 in head length (H.L.). Peduncle length 1.06 in H.L.

SKIN AND SCALES: About eight series of body scales from lateral line to dorsal origin, about 12 series from lateral line to anal origin, about 54 series from occiput to dorsal origin, and about 70 rows from dorsal origin to adipose. Body scales in vicinity of lateral line much smaller than lateral line scales. Lateral line scales relatively small, numbering 66 in one known adult specimen. Lateral line scale above anal origin: H/L .753; T/L .350; P/L .168, shape of lateral line scale similar to *B. infans.* Lateral line scale above pectoral insertion: H/L .816; T/L .332; P/L .166. Penultimate lateral line scale: H/L 1.06. Ultimate lateral line scale missing, due to damage.

HEAD: Dorsal profile essentially horizontal. Snout length greater than eye diameter. Postorbital head depth less than body depth, head width subequal to body width. Eyes directed vertically. Head length 5.79 in S.L. Snout length 3.03 in H.L. Horizontal eye diameter 4.06 in H.L. Postorbital head length 2.31 in H.L. Interorbital width 11.2 in H.L. Dense pigment covering entire head.

Subopercle larger than opercle, both bones plowshare shaped, rounded and nonserrate posteriorly.

Pseudobranchiae well-developed, 15 long filaments in adult specimen. Gill filaments moderately long extending to posterior border of gill covers. Gill membranes united under posterior margin of orbit.

MOUTH: Upper jaw length 1.39 in H.L. Lower jaw length 1.23 in H.L. Upper jaw terminating below posterior border of eye.

Premaxillary tooth count: 59. Dentary teeth 44 lateral, 10 medial. Palatine teeth 15, 5 larger teeth medial to 10 lateral teeth. Lingual teeth 11, none of them strongly hooked.

FINS: Dorsal moderately high, length of longest dorsal ray 10.6 per cent S.L., length of dorsal base 4.9 per cent S.L. Appressed pelvics not quite reaching one-half pelvic - anal distance. Appressed pectorals not reaching pelvic insertion. Anal fin base elongate, length of base 24.7 per cent of S.L. Anal origin well behind midlength, preanal distance 62.8 per cent S.L.

COLOR: Color in alcohol a uniform dull brown, with slight enhancement of pigment lining scale pockets. Fins all densely pigmented. Peritoneum intense black.

Development.—B. linguidens is known from a total of 14 specimens: holotype and paratypes of B. linguidens [Mead and Böhlke, 1953, p. 241; 1 (47.3) + 2 (38.2-38.8)], syntypes of B. diaphana Rass [1955, pp. 329-330; 2 (55.5-77.4)], and the 8 (48.0-85.5) larvae and 1 (221.0) adult reported in the present work. Larvae of B. linguidens are distinguished by the following combination of characters: pelvic insertion well in advance of dorsal origin, no pigment on body or head (other than eye) prior to metamorphosis, 28-30 anal rays, 24-25 pectoral rays. In my material all fin rays fully formed. Subsequent course of growth and especially metamorphosis unknown, but undoubtedly similar to other species of Benthalbella.

Distribution.—B. linguidens is known only from the subarctic North Pacific (fig. 19), north of 39° 21' N, from off northern Japan to off Oregon. It is not known from off California. The holotype came from 13 m. of water or less and the paratypes from 66-100 m. of water or less (Mead and Böhlke, 1953, p. 241). All three were captured at night. Larval material I have seen came from three night-time hauls: 0-209 m., 0-204 m., and 0-3660 m. The single adult came from a haul from 0-1000 m. Larvae of *B. linguidens* thus occur in the upper 100 m., a considerably shallower depth than the minimum known depth for larvae of *B. dentata.* Larvae of *B. linguidens* have been captured from May through September (but only 13 are known).

Material examined.—NMFS: HMS 30-33, 5 (72.9-78.9); HMS 30-88, 1 (85.5). OSU 568, 1 (221.0). SIO53-340, 2 (48.0-48.9). USNM 163281, 47.3, holotype.

A total of 10 (47.3-221.0) specimens from five collections.



FIG. 26. Benthalbella macropinna Bussing and Bussing. A. Paratype, LACM 10135, 179 (alter Bussing and Bussing, 1966, text-fig. 1). B. Lateral line scale above analorigin, LACM 10135, 178.6. C. Lateral line scale above pectoral insertion, USC-E 563, 221.0. D. Penultimate lateral line scale, USC-E 2241, 129.7. E. Ultimate lateral line scale.

Benthalbella macropinna Bussing and Bussing, 1966. Figure 26.

Benthalbella macropinna Bussing and Bussing, 1966, pp. 53-64.

Holotype.—LACM 10118, 209 mm. S.L. USNS Eltanin sta. 359. Scotia Sea, 56° 17' S, 58° 09' W, (1KMT: 0-840 m) December 6-7, 1962.

Comparative diagnosis.—A species of Benthalbella with 5-6 dorsal rays, 35-39 anal rays, 25-27 pectoral rays, and 62-65 lateral line scales. The combination of these characters distinguishes *B. macropinna* from all other known scopelarchids.

Description.—Based on 2 (29.1-32.5) larvae, 11 (65.1-90.5) metamorphosing specimens, and 50 (86.2-233.5) adolescents and adults. With the exception of meristic characters, the description given first is that based on adults, followed by an account of development. MERISTIC CHARACTERS: Values for the holotype (taken from Bussing and Bussing, 1966, pp. 53-64) given in parentheses. Dorsal 5-6 (5); anal 35-39 (37); pectoral 25-27 (26); lateral line scales 62-65; vertebrae 60-62.

PROPORTIONAL DIMENSIONS: Based on 12 (86.2-220.0) specimens: ISH 1560, 1 (220.0); LACM 10129, 1 (134.1), paratype; LACM 10135, 1 (178.6), paratype; LACM 10136, 1 (131.0), paratype; SIO61-42, 1 (188.0), paratype; SOSC-E 20-15, 1 (94.2); USC-E 1163, 1 (136.0); USC-E 1671, 1 (113.5); USC-E 1676, 1 (123.6); USC-E 1689, 1 (118.0); USC-E 2242, 1 (154.0); USC-E 2244, 1 (86.2). Expressed as thousandths of the S.L. and given as the mean, range (values in parentheses), and values for the holotype (taken from Bussing and Bussing, 1966).

Body, depth at dorsal origin, 140 (115-192) 152. Caudal peduncle: least depth, 49 (43-55) 48; length, 80 (74-86). Adipose fin: distance to midcaudal rays, 122 (115-132); length of base, 41 (27-65); length of fin, 46 (32-53). Anal fin: length of base, 415 (400-432); length of longest ray, 105 (73-120). Dorsal fin: length of base, 17 (15-21); length of longest ray, 57 (40-66); dorsal origin to anal origin (distance between verticals), 200 (185-220); end of dorsal base to base of midcaudal rays, 676 (663-701). Pectoral fin, length of longest ray, 96 (72-118). Pelvic fin, length of longest ray, 171 (139-197). Pelvic insertion to anal origin, 231 (204-261) Pectoral insertion to pelvic insertion, 111 (99-124). Anus to anal origin, 26 (13-48). Distance from snout to: anus, 510 (464-535); dorsal origin, 315 (281-335) 297; anal origin, 533 (505-547) 526; pectoral insertion, 201 (169-213) 190; pelvic insertion, 308 (273-330) 299; anterior margin of eve, 53 (45-57) 49. Head length, 199 (170-212) 190. Postorbital head length, 66 (59-70) 93. Eve: horizontal diameter, 79 (66-93) 69; vertical diameter, 76 (64-85). Interorbital width, 11 (9-13) 11. Upper jaw length, 148 (129-157) 138. Lower jaw length, 165 (150-174) 158. Longest dentary tooth, 25 (23-28).

BODY: Body deep, strongly compressed. Body depth 7.07 (5.21-8.71) in S.L. Peduncle depth 4.04 (3.14-4.82) in head length (H.L.). Peduncle length 2.46 (2.06-2.70) in H.L.

SKIN AND SCALES: Body scales relatively small, seven or more rows from lateral line to dorsal origin, 10 or more rows from lateral line to anal origin. Lateral line scales moderate in size but much larger than adjacent body scales, numbering 62-65 in 17 specimens counted. Lateral line scale above anal origin based on 10 (131.0-221.0) specimens: H/L 1.21 (1.11-1.30); T/L .684 (.511-.801); P/L .433 (.333-.505); height of scale slightly exceeding length, tympanum alate, not covering large central pore anteriorly. Lateral line scale above pectoral insertion, based on 2 (215.0221.0) specimens and listed in that order: H/L 1.15, .960; T/L .575, .506; P/L .351, .278. Penultimate lateral line scale based on 4 (129.7, 187.0, 220.0, 221.0) specimens and listed in that order: H/L .861, .890, .940, 1.00; T/L .522, .621, .582, .671; P/L .432, .397, .462, .358. Ultimate lateral line scale based on 3 (129.7, 136.0, 220.0) specimens and listed in that order: H/L .567, .676, .505; imperforate.

HEAD: Dorsal profile forming gently rounded arch over eye, descending rather steeply to snout. Eye diameter exceeds snout length. Head depth behind eye subequal to body depth in smaller specimens, but considerably less than body depth in largest adults. Postorbital head width subequal to body width. Head length 5.10 (4.71-5.88) in S.L. Snout length 3.76 (3.41-4.37) in H.L. Horizontal eye diameter 2.45 (2.29-2.70) in H.L. Postorbital head length 3.03 (2.65-3.51) in H.L. Interorbital width 17.6 (15.6-21.3) in H.L.

Head densely pigmented on all external surfaces, on branchiostegal membranes and within branchial cavity, but little or no pigment within oral cavity. Especially dense pigment bordering orbit, on snout, and lining dentigerous portions of jaws. A dense cap of enlarged black melanophores at dorsal margin of pearl organ.

Opercle and subopercle subequal in size, both with rounded nonserrate posterior margins. Pectoral insertion opposite deep notch at opercle-subopercle border.

Pseudobranchiae well-developed, counts based on 3 (116.0-188.0) specimens and listed in that order: 10, 11, 11. Gill filaments relatively short, not reaching posterior border of gill covers. Gill membranes united under anterior margin of eye.

MOUTH: Upper jaw length 1.33 (1.27-1.45) in H.L. Lower jaw length 1.19 (1.13-1.28) in H.L. Upper jaw terminating below posterior margin of orbit.

Tooth counts based on 3 (113.5, 136.0, 188.0) specimens and listed in that order. Premaxillary tooth counts: 41, 50, 60. Dentary tooth counts: lateral, 28, 30, 45; medial, 10, 14, 12. Palatine tooth counts: 12, 15, 15. Lingual tooth counts: 13, 12, 13. Basihyal teeth hooked and lanceolate, decreasing in length but more strongly hooked posteriorly. Longest dentary tooth 7.75 (6.56-8.95) in H.L.

FINS: Dorsal short, length of longest ray 5.7 (4.0-6.6) per cent S.L., length of base 1.7 (1.5-2.1) per cent S.L. Adipose fin merging anteriorly with low fatty middorsal ridge extending to nearly over anus. Appressed pelvic fins reaching slightly more than half-way to anal origin. Appressed pectoral fins not reaching one-half distance between pectoral insertion and pelvic insertion. Anal base extremely elongate, length of base 41.5



(40.0-43.2) per cent S.L. Anal origin at approximately midlength, a unique feature of this species, preanal distance 53.3 (50.5-54.7) per cent S.L.

COLOR: Color in alcohol a uniform dull brown but with scale pockets distinctly outlined by heavier pigmentation. Pigment present on all fins. Color of younger adults a brassy-brown, with an iridescent guanine layer present on forepart of body (Bussing and Bussing, 1966). Pigment at base of pectorals, but apparently lacking on rays and membranes. Peritoneum a dense uniform black.

Development.—The description of development in *B. macropinna* is based on 2 (29.1-32.5) larvae, 11 (65.1-90.5) metamorphosing specimens, and 9 (86.2-120.5) adolescents. Figure 27 illustrates development in *B. macropinna*.

RECOGNITION: Larvae of *B. macropinna* are distinguished by the following combination of characters: origin of pelvic fin buds beneath dorsal base, but pelvic insertion in adults distinctly ahead of dorsal origin; pigment present on pectoral fin, as scattered fine melanophores, prior to ossification of pectoral fin rays, but not after; dorsal 5-6; anal 35-39.

FINS: In the two larval specimens only the caudal rays are ossified but the dorsal and adipose fins are not connected by a continuous finfold. Procurrent caudal rays connected by continuous finfold with dorsal adipose and anal fin. Anal rays unossified but anal radials easily distinguishable. Pelvic fins appear as buds at ventrolateral body contour, beneath level of intestine, and beneath dorsal base. Dorsalmost pectoral rays beginning to form. Order of ossification of fin rays unknown but probably similar to other species of *Benthalbella*.

METAMORPHOSIS: 7 (65.1-78.5) Onset of metamorphosis indicated by appearance of two rather dense patches of peritoneal pigment, midlaterally on each side of gut between pectoral fin base and extending posteriorly to one-half pectoral-pelvic distance. Although these patches resemble peritoneal sections of larvae of other genera, the margins, in these, the two smallest specimens, are indistinct, with central area of patch densely pigmented but peripheral areas with scattered melanophores, indicating, in my opinion, rapid growth of the pigmented area. This is corroborated by peritoneal patches expanding to form a complete tube around gut in specimens 78-83 mm.; the tube of peritoneal pigment expanding posteriad with rearward elongation of intestine. Coincident with appearance of peritoneal pigment are elongations of the caecum and the intestine which continue until the anus lies immediately in advance of the anal origin and the caecum just slightly anterior to the anus.



F1G. 28. Distribution of *B. macropinna* Bussing and Bussing. Closed circles: records based on metamorphosing specimens and adults. Inset: additional records of *B. macropinna* (circles) and *B. elongata* (triangles) from South Atlantic Ocean. Open circles represent positions of capture of two known larvae of *B. macropinna*. Closed circles represent adults of *B. macropinna*. Closed circles with small open triangles represent capture of adult *B. elongata* and *B. macropinna* in same haul.

4 (83.2-90.5). Initial head and body pigmentation appearing as blotch of melanophores at dorsoposterior corner of orbit, on occiput and on snout. Pearl organ first appears in metamorphosing specimens.

ADOLESCENTS: 9 (86.2 - 120.5). Completion of metamorphosis taken to be point of maximum rearward elongation of gut and caecum, as well as peritoneal pigment. *B. macropinna* differs from its congeners in that full adult pigmentation is acquired subsequent to metamorphosis. Adolescents of this species retain a distinctly larval appearance well after metamorphosis, and the smallest specimen I have seen with full adult pigmentation is one 188.1 mm. in length. In adolescents head pigmentation expands to cover head with intense pigment around orbit, on snout, lining jaws, and forming the cap of melanophores over the pearl organ. Body pigmentation appears middorsally just behind occiput and expands rearward with subsequent growth to cover body dorsal to lateral line. Pigment associated with lateral line appears as fine black dots or spots, one per scale pocket, and apparently expands to fully outline scale pockets as in adults. Pigment at base of anal fin appears as black melanophores over the proximal anal radials of the anteriormost 5-6 anal rays in specimens 86 mm. and larger, and expands rearward over the base of the anal fin. Muscle tissue begins invasion of abdominal body wall at about time of appearance of pigment on anal base.

Distribution.—B. macropinna is an Antarctic species, no doubt circumpolar throughout subantarctic and antarctic waters in the Antarctic Circumpolar Current. Only four specimens, two adults and two larvae (fig. 28), have been taken north of the Subtropical Convergence, and these were taken from the area of the Benguela Current. B. macropinna is known from 27° 10' S, 08° 59' E to 66° $08' - 65^{\circ}$ 51' S, 82° 32 - 38' W, in the north-south direction, and from ca. 177° E to ca. 09° E, in the South Pacific and South Atlantic. It has not yet been taken, but undoubtedly occurs, in the southern Indian Ocean.

The two larvae, taken in January and February, were taken from two tows: 1000 mwo and 1500 mwo. Only two adults have ever been taken in hauls to less than 500 m: 1 (107.2) day-time, 0.270 m; 1 (188.1), time unknown, 0-100 m.

Material examined.-A total of 63 (29.1-233.5) specimens from 47 collections, DANA: D3975 IV, 1 (29.1); D3979 1, 1 (32.5). ISH: ISH 1560, 3 (215.0 - 220.0); ISH 412 71, 3 (219 - 233.5); ISH 557 (71, 2 (222.5-225); ISH 629/71, 3 (218-228.5); ISH 849 71, 2 (225-230.5); ISH 920/71, 1 (217.5); ISH 1048/71, 1 (225.5). ISH 1050 71, 2 (66.6-74.5); ISH 1133 71, 3 (210-227); ISH 1229/71, 2 (196.5-202.5); ISH uncat. WH 367 71, 1 (65.1). LACM: LACM 10127, 1 (105.3) paratype; LACM 10128, 1 (90.0) paratype; LACM 10129, 1 (139.1) paratype; LACM 10132, 1 (90.5) paratype; LACM 10135, 1 (178.6) paratype; LACM 10136, 1 (131.0) paratype; LACM 10137, 1 (ca. 190) paratype; LACM 10141, 2 (84.8-85.8) paratypes. SIO: S1O61-42, 1 (188.0) paratype. SOSC (all station numbers given are Elianin field numbers): E20-15, 1 (94.2); E 2254, 1 (188.8); E 2257, 2 (70.2-74.5); E 2263, 3 (92.0-128.1); E 2289, 2 (70.8-78.5); E 2294, 1 (135.0); E 2301, 1 (83.2). USC (alt station numbers given are Eltanin field numbers): E 563, 1 (221.0) paratype; E 1163. 1 (136.0); E 1187, 1 (ca. 88.0); E 1220, 1 (107.2); E 1269, 1 (98.9); E 1307, 1 (116.0); E 1615. 1 (187.0); E 1623, 1 (127.5); E 1671, 1 (113.5); E 1676, 1 (123.6); E 1689, 1 (118.0); E 2177. 1 (134.5); E 2189, 1 (132.8); E 2241, 1 (129.7); E 2242, 1 (154.9); E 2244, 1 (86.2). USNM: USNM 260173 F1, E 13-396, 1 (207) paratype; USNM 260173 F2, E 13-1162, 1 (135) paratype.

Rosenblattichthys Johnson 1974

Phanops Rofen 1963, p. 4; 1966, pp. 594-601 (in part, Phanops volucris Rofen). Rosenblattichthys Johnson 1974, p. 451.

Type-species .- Phanops volucris Rofen 1966, p. 595.

Diagnosis.—Scopelarchids with parietals present, antorbital present, ethmoid process on first infraorbital absent; basihyal short, lingual teeth extending to over second basibranchial; suspensory pharyngobranchial present; coracoid expanded, coracocleithral fenestra small; 46-51 vertebrae; 47-53 lateral line scales; dermal pigment present but not concentrated in distinct stripes; supraorbital present; pelvic insertion in adults slightly in advance of dorsal origin; larvae with extremely deep bodies and elongate heads, HL exceeding 30 per cent SL; pectoral fins precocious, developing before all other fins except caudal; larvae with one peritoneal section only; dorsal accessory pigment spots and areas well-developed, middorsal and midventral spots or areas (fig. 29) entirely in advance of end of adipose or last anal ray respectively; pelvic fin bud appearing midlaterally in abdominal cavity wall, beneath or behind dorsal base.

Description.—Frontals broad, interorbital area relatively broad and flat, restricted to anterior one-third of postorbital dorsal roof of skull; supraoccipital with crest-like ridge extending full length of bone and dividing posterior portions of frontal bones; opisthotics with anteroventrally directed projection; second and third infraorbitals both quite deep, longer in vertical than in horizontal dimension; supramaxilla large; opercle plowshare shaped, less than subopercle in size; hyomandibular with 4 rodlike arms; 3 extrascapular bones.

Dorsal 8-10, anal 21-24, pectoral 21-26, lateral line scales 47-53, vertebrae 46-51.

Body short, deep, massive, moderately compressed. Anus immediately in advance of anal origin. Lateral line scales above anal origin moderate in size, scale height subequal to length, height of tympanum 47-64 per cent scale length, tympanum alate, completely covering moderate sized pore, pore height 20-27 per cent scale length.

Interorbital broad. Dorsal profile rounded with moderate descent to rounded snout. Head depth and width behind orbit subequal to body depth and width. Gill membranes united under anterior margin of eye.

Dorsal moderately long, origin well before midlength. Pectorals and pelvics elongate, particularly so in *R. alatus:* pelvic length 34.3-47.2 per cent S.L. (*R. alatus*), 17.3 per cent S.L. (*R. hubbsi*), 16.5-22.2 per cent S.L. (*R. volucris*) pectoral length 28.5-31.6 per cent S.L. (*R. alatus*) 17.3 per cent S.L. (*R. hubbsi*), 17.4-23.2 per cent S.L. (*R. volucris*). Anal fin base short. Pigment present or absent on pelvics, present on pectorals. Pigment present on anterior anal rays and bases.

LARVAE: Body short, deep, with moderately deep peduncle, and extremely large head, head length exceeding 30 per cent S.L. in specimens up to 28 mm. or larger. Pectoral fins precocious, extremely prominent in



FIG. 29. Comparison of pigment patterns and larval morphology in two species of *Rosenblattichthys.* **A.** *R. volucris,* LACM 9638, 30.5. **B.** *R. alatus,* SOSC: AB 6-340 A, 20.7.

small larvae (fig. 29). Pelvic fin buds appear midlaterally above level of intestine beneath or slightly behind last dorsal ray. Dorsal adipose remains elongate, to over anal origin, in specimens up to 30 mm. in size. One peritoneal section. Accessory pigment spots and areas present and extremely prominent (fig. 29), middorsal and midventral pigment spots or areas (DA, DAA, AA, PA) entirely ahead of end of adipose base or end of anal base respectively. Metamorphosis gradual.

KEY TO THE SPECIES OF Rosenblattichthys (specimens 40 mm. and larger)

1.	Pigment lacking on pelvic fins, branchiostegal membranes covered medially with
	dense black pigment R. volucris (Rofen)
	Transitional waters of eastern Pacific, equatorial eastern Pacific.
	Pigment present on pelvic fins, branchiostegal membranes lacking pigment med-
	ially
2(1).	A dense black band of pigment extending from bases of anterior anal rays interior
	to hypaxial and epaxial body musculature emerging middorsally above anal origin.
	pelvic fins extending far beyond anal origin R. alatus (Fourmanoir)
	IndoPacific; north, south, and equatorial central Pacific.
	No dense black band of pigment internal to body musculature, pelvic fins not reach-
	ing anus
	Equatorial Atlantic.

The following key to larval and metamorphic specimens of *Rosenblattichthys* does not include *R. hubbsi*, known only from the 144.5 mm. S.L. holotype. The putative larvae of *R. hubbsi*, discussed in the account of that species, agree most closely with the larvae of *R. alatus* in the characters given below.

> KEY TO LARVAL AND METAMORPHIC SPECIMENS OF Rosenblattichthys (specimens 10-11 mm. and larger)

Rosenblattichthys alatus (Fourmanoir) 1970. Figure 30.

Benthalbella alata Fourmanoir 1970, pp. 23-24.

Holotype.—Orstom Cyclone VI—2. 48 mm. S.L. Western equatorial Pacific, 00° 18' S, 169° 57' E, September 2, 1967. Holotype deposited in Museum d'Histoire Naturelle de Paris, No. 1970-36.



FIG. 30. Rosenblattichthys alatus (Fourmanoir). A. Holotype, 48 mm. S. L. (after Fourmanoir, 1970, p. 23) B. Lateral line scale above pelvic insertion. ORSTOM MARURU 18A, 64.5.

Comparative diagnosis.—A species of Rosenblattichthys with 8-9 dorsal rays, 20-24 anal rays, 22-26 pectoral rays, and 47-49 lateral line scales (based on four specimens). Pelvic and pectoral fins extremely elongate, covered with dense black pigment, the pectorals slightly less than and the pelvics greater than one-third the S.L. in length. A dense black bar of pigment extending from bases of anterior anal fin rays interior to hypaxial and epaxial muscles and emerging middorsally above

anal origin. The combination of these characters distinguishes R. alatus from all other known scopelarchids.

Description.—Based on 20 (9.0-28.1) larvae and 6 (39.9-80.1) adolescents. With the exception of meristic characters, the description given first is based upon the adolescents, followed by an account of development.

MERISTIC CHARACTERS: Values in parentheses are those of the holotype (taken from Fourmanoir, 1970, pp. 23-24). Dorsal 8-9 (9); anal 20-24 (21); pectoral 22-26 (25); lateral line scales 47-49 (based on four specimens); vertebrae 46-47 (based on two specimens).

PROPORTIONAL DIMENSIONS: Based on 5 (39.9, 40.5, 47.4, 64.5, 80.1) specimens and listed in that order: DANA 3814 1, 1 (39.9); DANA 3906 111, 1 (47.4); ORSTOM MARURU 18A, 1 (64.5); S1070-343, 1 (40.5); S1072-317, 1 (80.1). Measurements expressed as thousandths of the S.L.

Body, depth at dorsal origin, 163, 175, 171, 195, 200. Caudal peduncle: least depth, 88, 86, 82, 87, 85; length, 95, 99, 116, 93, 111. Adipose fin: distance to midcaudal rays, 160, 160, 169, 184, 165; length of base, -, 37, 63, 46, 51; length of fin, -, 49, 84, 64, 69. Anal fin: length of base, 261, 249, 253, 248, 282; length of longest ray, 138, 146, 147, 130, 137. Dorsal fin: length of base, 50, 49, 55, 48, 44; length of longest ray, 90, 91, 95, 85, 112; dorsal origin to anal origin (distance between verticals), 231, 257, 245, 254, 237; end of dorsal base to base of midcaudal rays, 526, 531, 538, 567, 551. Pectoral fin, length of longest ray, 301, 309, 316, 285, 293. Pelvic fin, length of longest ray, 398, 472, 380, 343, 315. Pelvic insertion to anal origin, 213, 237, 232, 242, 256. Pectoral insertion to pelvic insertion, 203, 188, 169, 188, 187. Anus to anal origin, 50, 57, 51, 54, 56. Distance from snout to: anus, 627, 617, 591, 605, 594; dorsal origin, 446, 457, 453, 419, 423; anal origin, 677, 674, 643, 660, 639; pectoral insertion, 286, 272, 296, 256, 256; pelvic insertion, 466, 432, 432, 415, 418; anterior margin of eye, 88, 86, 95, 73, 69. Head length, 248, 249, 264, 231, 226. Postorbital head length, 80, 74, 95, 84, 77. Eye: horizontal diameter, 75, 81, 78, 78, 86; vertical diameter, 75, 86, 80, 79, 87. Interorbital width, 38, 37, 21, 19, 15. Upper jaw length, 178, 175, 179, 161, 165. Lower jaw length, 198, 198, 194, 172, 182. Longest dentary tooth, 20, 25, 30, 20, 25.

BODY: Body depth 5.00-6.85 in S.L. Peduncle depth 2.66-3.21 in head length (H.L.). Peduncle length 2.03-2.60 in H.L.

SKIN AND SCALES: Except for a very few scale pockets on several specimens, all scales and scale pockets (except lateral line scale pockets) missing on specimens I have examined, no doubt due to damage. Lateral line scales (determined from scale pockets) 47-49 in four specimens counted. All lateral line scales lost in all specimens examined except two
scales present above pelvic insertion on right side of one specimen (MARURU 18A, 64.5). The anteriormost of these two scales is figured (fig. 30B) and the measurements are as follows: H/L 1.00; T/L .642; P/L .268; height of scale equal to width, tympanum rounded anteriorly and moderately alate, completely covering moderately deep central pore.

HEAD: Eye in largest (80.1) specimen exceeds snout length, but eye diameter less than snout length in 47.4 mm. S.L. specimen and smaller specimens. Eyes moderately large, directed straight upward. Head length 3.79-4.42 in S.L. Snout length 2.78-3.29 in H.L. Horizontal eye diameter 2.62-3.37 in H.L. Interorbital width 6.60-15.1 in H.L.

Head with pigment on occiput, dorsoposterior corner of orbit, snout, and with a unique bar of enlarged black melanophores bordering medial surface of posterior border of opercle, subopercle, and posterior edge of branchiostegal membranes.

Subopercle larger than opercle, both bones rounded posteriorly. Pectoral insertion opposite a V-shaped notch at opercle-subopercle border.

Pseudobranchiae well-developed, counts based on 2 (47.2-64.5) specimens and listed in that order: 12, 12. Gill filaments relatively elongate, extending slightly beyond posterior border of gill cover.

MOUTH: Upper jaw length 1.37-1.47 in H.L. Lower jaw length 1.24-1.36 in H.L. Upper jaw terminating slightly anterior to a vertical through posterior margin of orbit.

Tooth counts based on 3 (39.9, 47.2, 64.5) specimens and listed in that order. Premaxillary tooth counts: 25, 45, 40. Dentary tooth counts: lateral, 29, 25, 20; medial, 9, 9, 13. Palatine teeth arranged more or less in two irregular series, counts given as lateral—medial, 8 (arranged in one series), 10-5, 11-4. Lingual tooth counts: 9, 12, 11. Lingual teeth restricted to basihyal in larvae. Basihyal remaining relatively elongate, at least in specimens up to 80.1 mm. S.L., with at most 3-4 teeth over first basibranchial. Presumably lingual teeth appear more posteriorly over basibranchials in adults. Longest dentary tooth 8.94-12.4 in H.L.

FINS: Longest dorsal ray 8.5-11.2 per cent S.L. Dorsal base 4.4-5.5 per cent S.L. Pelvics extremely elongate, exceeding one-third of S.L. Length of longest pelvic ray 31.5-47.2 per cent S.L. Length of longest pectoral ray 28.5-31.6 per cent S.L. Appressed pelvic fins reaching far beyond anal origin, appressed pectoral fins nearly reaching anal origin.

COLOR: Color in adolescents apparently limited to fins, internal black bar between anterior anal fin and middorsal contour, and head pigment as described above and in comparative diagnosis. A bar of pigment present internally over bases of caudal rays. Peritoneum dense black.



FIG. 31. Development of *R. alatus* (Fourmanoir). A. Putative larva, DANA 39291, 10.5. B. Larva, S1060-130, 19.5. C. Adolescent, S1070-343, 40.5.

Development.—The description of development in *R. alatus* is based on 20 (9.0-28.1) larvae and is illustrated in Figure 31.

RECOGNITION: Larvae of *R. alatus* are distinguished by the following combination of characters: dorsal 8-9, anal 20-24, pectoral 22-26; head length in larvae up to 20 mm. exceeding 30 per cent of S.L.; pectoral fins precocious, ossification of pectorals prominent in very small larvae (fig. 31) and precedes all other fins except caudal; unique combination of up to five accessory pigment spots or areas, one middorsal appearing over posterior one-third of anal base (DA), one appearing as a single oblong dash at fork of caudal fin (CA); two areas on anal base, one on anterior portion of anal base (AA) and one over posterior onethird of base (PA); and a single spot on ventral contour of intestine just anterior to vent (1A). Differences between the larvae of *R. alatus* and the putative larvae of *R. hubbsi* are discussed in the account of the latter species. FINS: In smallest available specimen (9.0 mm.) dorsal two-thirds of pectoral fin with ossified rays, remaining fins lacking ossified rays. Pectoral fins precocious, appearing very early in development, and extremely prominent in small larvae. Pelvic fins appearing midlaterally beneath or just behind last dorsal ray, pelvic insertion beneath middle of dorsal base in large larvae. Ventral adipose fin never exceeding one-half pelvic-anal distance, reduced to a thin triangular flap in specimens exceeding 18-20 mm. Dorsal adipose remains elongate, to over anterior anal rays, in largest larvae. All fin rays ossified in specimens exceeding 18-20 mm. Order of fin ray ossification: pectoral, caudal, dorsal, anal, pelvic.

PERITONEAL SECTIONS: Only one peritoneal section. Peritoneal section present in smallest larvae (9.0, 10.0) as thin, dark brown, transverse sheet, above gut, and medial to pectoral fin base, expanding posteriad with subsequent growth to form a canopy above gut before expanding laterad to form tube around gut.

ACCESSORY PIGMENT SPOTS OR AREAS: A maximum of five pigment spots or areas as described above, and illustrated in Figures 29 and 31: DA, CA, PA, AA, IA. All pigment spots lacking in two of the smallest larvae (9.0, 10.5) and only pigment present is that of eyes and single peritoneal section. First accessory spots to develop are DA and CA, present in all larvae exceeding 10-11 mm. in size. Smallest larva with an IA present with 11.1 mm., but an IA was present in only 6/17 larvae, and may either be easily lost due to damage, or may be irregularly present or absent. Anal pigment areas (AA, PA) present in all larvae exceeding 14-15 mm. in size. In subsequent growth, DA comes to lie over anterior anal rays, and is connected by internal black bar of pigment to pigment over anterior anal ray bases. CA not present in adolescents but is replaced by a bar of enlarged black melanophores along the bases of the caudal rays.

DERMAL PIGMENTATION: Dermal pigmentation absent in all larval specimens and adolescents.

GUT: Post-pelvic gut length about one-half pelvic-anal distance in smaller larvae, reaching maximum rearward extent (to just before anal origin) in 15-20 mm. larvae. Caecum visible only as a short blind sac, protruding from gut. Caecum expands during metamorphosis, reaching to just before anus in largest specimens.

METAMORPHOSIS: *R. alatus* exhibits gradual metamorphosis with changes leading to adult morphology occurring over a wide size range. These changes include at least the following: reabsorption of ventral adipose fin, decrease in length of base of dorsal adipose fin, extensive



FIG. 32. Distribution of Rosenblattichthys alatus and R. hubbsi. Circles: R. alatus. Triangle: R. hubbsi, holotype. Open symbols: records based solely on larvae. Closed symbols: records based on adolescents. Open triangles: putative larvae of R. hubbsi. posteriad expansion of caecum and peritoneal pigment, appearance of distinctive pigmentation of adolescents, and invasion of abdominal body wall by muscle tissue. Based on my material, these processes begin in this species as early as specimens 20 mm. in size, and are not complete in any of the adolescent specimens.

Distribution.—R. alatus is known from a total of 28 (9.0-80.1) specimens from the Pacific and Indian Oceans (fig. 32). R. alatus occurs throughout the Indian Ocean from 25° 19' S, off Africa, to 5° 59' N, near Sumatra. From the Pacific R. alatus is known from the South China Sea, Philippine Sea, and Central Pacific to 150° W.

Larvae of R. *alatus* have been captured throughout the year in hauls to depths as shallow as 25-30 m. Adults have not been taken in hauls less than 200 m. in depth, but only eight young adults are known for this species.

Material examined.—A total of 26 (9.0-80.1) specimens from 24 collections. **DANA:** D 3814 I, 1 (39.9); D3893 I, 1 (11.1); D3903 II, 1 (21.0); D3906 III, 1 (47.4); D3921 III, 2 (24.0-28.1); D3921 V, 1 (15.4); D3921 VIII, 1 (14.6); D3925 IV, 1 (15.1); D3927 II, 1 (9.0); D3928, 1, 1 (12.1); D3929 I, 1 (10.5); D3932 VIII, 1 (18.9); D3932 VIII, 1 (10.0); D3964 II, 2 (13.4-15.0). **ORSTOM:** MARURU 18A, 1 (64.5). **SIO:** S1O60 - 130, 1 (19.5); S1O70-310, 1 (18.0); S1O70-343, 1 (40.5); S1O70-344, 1 (21.1); S1O71-295, 1 (25.6); S1O72-9, 1 (21.2); S1O72-317, 1 (80.1). **USNM:** AB 6-340A, 1 (20.7). **WHOI:** AB 6-335, 1 (53.5).

Rosenblattichthys hubbsi Johnson 1974. Figure 33.

Rosenblattichthys hubbsi Johnson 1974, p. 452.

Holotype.—ISH 2219/71. 144.5 mm. S.L. Equatorial Atlantic, 02° 27' S, 19° 00' W (CMBT 1600: 0-657 m.); April 10, 1971. The holotype is the only known specimen of *R. hubbsi*.

Comparative diagnosis. A species of Rosenblattichthys with 8 dorsal rays, 24 anal rays, 21 pectoral rays, 53 lateral line scales; pelvic and pectoral fins moderately elongate, 17.3 per cent S.L. and equal in length in the holotype; both pectoral and pelvic fins covered with small scattered melanophores (cf. covered with dense black pigment in *R. alatus*, pelvic fins lacking pigment in *R. volucris*); a streak of dense black pigment bordering anterior margin of eye (absent in *R. alatus*); no bar of internal pigment extending dorsad from anterior anal fin ray bases; pigment lacking on branchiostegal membranes; pelvic insertion just anterior to a vertical through dorsal origin. The combination of these characters distinguishes *R. hubbsi* from all other known scopelarchid species.

Description. Based on the 144.5 mm. S.L. holotype.

MERISTIC CHARACTERS: Dorsal 8; anal 24; pectoral 21; lateral line scales 53; vertebrae 49.



F1G. 33. Rosenblattichthys hubbsi Johnson 1974. A. Holotype, 144.5 mm. S. L. B. Lateral line scale above anal origin, from holotype.

PROPORTIONAL DIMENSIONS: Expressed as thousandths of the S.L. Body, depth at dorsal origin, 170. Caudal peduncle: least depth, 82; length, 111. Adipose fin: distance to midcaudal rays, 140; length of base, 32; length of fin, 50. Anal fin: length of base, 242; length of longest ray, 104. Dorsal fin: length of base, 56; length of longest ray, 104; dorsal origin to anal origin, (distance between verticals), 264; end of dorsal base to base of midcaudal rays, 535. Pectoral fin, length of longest ray, 173. Pelvic fin, length of longest ray, 173. Pelvic insertion to anal origin, 278. Pectoral insertion to pelvic insertion, 153. Anus to anal origin, 702; pectoral insertion, 291; pelvic insertion, 436; anterior margin of eye, 84. Head length, 227. Postorbital head length, 91. Eye: horizontal diameter, 59; vertical diameter, 53. Interorbital width, 22. Upper jaw length, 174. Lower jaw length, 197. Longest dentary tooth, 48.

BODY: Body depth 5.90 in S.L. Peduncle depth 2.76 in H.L. Peduncle length 2.04 in H.L.

SKIN AND SCALES: About five series of body scales from lateral line to dorsal origin, about eight series from lateral line to anal origin. About 25 series of scales from occiput to dorsal origin and about 54 series from dorsal origin to adipose fin. Body scales adjacent to lateral line much smaller than lateral line scales. Lateral line scales relatively small, numbering 53 in holotype. Lateral line scale above anal origin: H/L .995; T/L .515; P/L .202; height of scale about equal to length of scale; anterior margin of tympanum more or less concave, with lateroanterior margins noticeably prolonged; tympanum irregularly alate posteriorly, completely covering central pore. Pectoral, penultimate, and ultimate lateral line scales missing in holotype due to damage.

HEAD: Snout length exceeding high diameter. Eyes moderately large, directed straight upward. Pearl organ essentially elliptical with major axis normal to visual axis of eye. Head length 4.40 in S.L. Snout length 2.69 in H.L. Horizontal eye diameter 3.86 in H.L. Interorbital width 10.2 in H.L.

Head with densely pigmented areas on occiput, interorbital, snout, around orbit, and lining gape and lateral surface of lower jaw. A band of dark black pigment bordering anterior margin of eye. Pigment on midventral line anterior to union of gill membranes. Branchiostegal membranes unpigmented.

Subopercle larger than opercle, both bones rounded posteriorly. Pectoral insertion opposite a V-shaped shallow notch at opercle-sub-opercle border.

Pseudobranchiae well-developed with 25 filaments on right side. Gill filaments moderately elongate, probably not reaching beyond posterior border of gill cover in life (the holotype is partly damaged and the normal posterior extent of the gill filaments can not be determined).

MOUTH: Upper jaw length 1.31 in H.L. Lower jaw length 1.16 in H. L. Upper jaw terminating at a vertical through posterior margin of eye.

Premaxillary teeth 52. Dentary teeth: lateral 40, medial 4. Palatine teeth, in one irregular series, 11. Lingual teeth 9, 5 over basihyal and 4 over first two basibranchials. Longest dentary tooth 4.69 in H.L.

FINS: Longest dorsal ray 10.4 per cent S.L. Dorsal base 5.6 per cent S.L. Adipose to caudal distance 14.0 per cent S.L., less than in *R. alatus* (16.0-18.4 per cent S.L.) but slightly greater than in *R. volucris* (12.4-14.3 per cent S.L.). Pelvic and pectoral fins equal in length in holotype, 17.3 per cent S.L. Appressed pelvic fins reaching slightly beyond one-half the distance between pelvic insertion and the anus. Appressed pectoral fins reaching slightly beyond pelvic insertion.

COLOR: Color in alcohol a more or less uniform yellow-brown with more intense pigmentation outlining scale pockets. Fin rays and membranes of all fins covered with finely scattered melanophores. Intense black pigment present at bases of dorsal, adipose and caudal fins. Midventral area with a ridgelike deposition of oil globules beneath the skin, extending from below pectoral base to anus. Peritoneum dense black.

Development.-

PUTATIVE LARVAE: Three larvae from two collections (DANA 1288 11, western equatorial Atlantic, 16° 04' N, 61° 52' W, S200: 1200 mwo, April 16, 1922, 1 (23.1); SIO69-26, Indian Ocean, 23° 18.8-22.1' S, 50° 40.4-27.8' E, 1KMT, September 27-28, 1968, 2 (17.8-27.2)) may belong to this species. Meristic characters: dorsal 9,9,9,; anal 23,24,24; pectoral 22.22.23. Counts of fin rays are not useful in distinguishing species of Rosenblattichthys and other meristic characters (lateral line scales, vertebrae, myotomes) cannot be determined on larvae. All three larvae possess only two accessory pigment areas, a single middorsal area (DA) appearing over posterior one-third of anal base, and a single oblong dash of pigment at fork of caudal (CA). These two pigment areas easily distinguish these three larvae from the larvae of R. volucris, but not R. alatus. All larvae of R. alatus larger than 10-11 mm. in size possess DA and CA pigment areas similar to those in the three putative larvae of R. hubbsi. However, all larvae of R. alatus exceeding 14-15 mm. in size also possess anal pigment areas (AA, PA), lacking in the putative larvae of R. hubbsi (17.8-27.2 mm. S.L.). Dermal pigmentation is lacking in larval and juvenile R. alatus but present in two (23.1, 27.2) of the putative larvae of R. hubbsi. In these specimens dermal pigmentation is present middorsally in two areas, one above the pectoral insertion, the other immediately posterior to the DA (smaller specimen), and occupies most of the surface of the body above the lateral line (larger specimen). In the larger specimen there is a noticeable gap in the pigmentation below the dorsal base, suggesting that the area covered by pigment expands anteriad and posteriad during growth from the posterior and anterior areas respectively seen in the smaller specimen.

All but the ventralmost pelvic rays and posteriormost anal rays are ossified in the smallest (17.8) specimen, but the course of fin ray ossification, especially the precocious development of the pectoral fins evidenced by these three specimens, is probably the same as in *R. alatus* and *R. volucris.* Only one peritoneal section. Anus immediately in advance of anal origin. Caecum in largest (27.2) specimen reaches one-third of the pectoral-pelvic distance but visible only as a short blind sac in the two smaller specimens.

The two specimens possessing dermal pigmentation are almost certainly the same species, and the characters discussed above as well as the capture of one of these specimens in the equatorial Atlantic strongly suggests that these specimens are young *R. hubbsi.* However, as *R.*

alatus is known from only 28 specimens (20 of these are larval), I am not willing to positively identify these three larval specimens as R. *hubbsi*. The resolution of this problem awaits additional material, especially from the Atlantic Ocean.

Distribution.—R. hubbsi is known only from the holotype taken in the central equatorial Atlantic (fig. 32).

Rosenblattichthys volucris (Rofen) 1966. Figure 34.

Phanops volucris Rofen, 1966e, p. 595; Craddock and Mead, 1970, p. 3.26.

Benthalbella linguidens (nec Mead and Bohlke, 1953): Fitch and Lavenberg, 1968, p. 51.

Neotype.—SIO64-28, 60.6 mm. S.L. Eastern North Pacific, 25' 28.9-35.3' N, 114° 06.6-113° 21.3' W (IKMT): 5500 mwo (60 min.) 4500 mwo (25 min.) 3500 mwo (35 min.) 2500 mwo (29 min.) 1500 mwo (30 min.) February 7, 1964.

Discussion.-Rofen (1966e, pp. 595, 601) in his key to the species of Phanops (= Scopelarchus) distinguished P. volucris from P. michaelsarsi (= S. michaelsarsi) and P. cavei (= S. michaelsarsi) by the following characters: anal 23-24, pectoral 26, pectoral fins colorless to light-brown on inner face, and by a number of proportional measurements. The locality for P. volucris was given as the eastern North Pacific. Rofen (1966e, p. 595) cites the name of this species as Phanops volucris Rofen 1963. However, in the 1963 paper, Rofen alludes only to "an undescribed species from the eastern North Pacific," providing neither a name nor a description of this species. The original description therefore is in the key in the 1966 paper. Deposited in the collections of the Scripps Institution of Oceanography are five scopelarchid specimens identified by Rofen that fit Rofen's (1966e) description of P. volucris, including one with a label designating it as the holotype (37.0 mm.), three (22.2-32.9) specimens identified as Scopelarchus volucris, and one (57.0) identified as Scopelarchus nicholsi (Parr). No mention of these or any other specimens of P. volucris appears in Rofen's 1966 paper. These five specimens are in fact R. volucris (Rofen) and establish with certainty the entity Rofen had in mind. It might also be mentioned that the nomen nudum listed in the genus Benthalbella (Rofen, 1966e, p. 573) is represented by a specimen at the California Academy of Sciences [CAS 63778, 1 (81.3)] with a label identifying it as the type of species. This specimen is also R. volucris.

The International Code of Zoological Nomenclature does not require reference to any extant material when proposing a new name at the species level. The description of *P. volucris* given by Rofen (1966e, pp. 595, 601) is sufficient to make this name available in that it follows the provisions of the *Code* given in Articles 10-15, and particularly in the sense of Article 13 a (i) is a statement purporting to give characters differentiating the taxon.

Although fixation of a type specimen is not a requirement of the *International Code* (Article 75), *R. volucris* is not only a poorly known deep-sea fish, but is the type species of *Rosenblattichthys*, and in connection with this revisionary work, I have designated the specimen listed above as the neotype of *Rosenblattichthys volucris* (Rofen).

Comparative diagnosis.—A species of Rosenblattichthys with 9-10 dorsal rays, 21-24 anal rays, 23-26 pectoral rays, 48-51 lateral line scales; pelvic and pectoral fins moderately elongate, 16.5-23.2 per cent S.L. in length, and subequal in length; pelvic fins lacking pigment; pelvic insertion just anterior to dorsal origin in adults. The combination of these characters distinguishes R. volucris from all other known scopelarchids.

Description.—Based on 87 (5.9-39.0) larvae and metamorphosing specimens and 21 (40.5-103.5) adults. With the exception of meristic characters, the description given first is that of the adults, followed by an account of development.

MERISTIC CHARACTERS: Values for the neotype given in parentheses. Dorsal 9-10 (9); anal 21-24 (23); pectoral 23-26 (25); lateral line scales 48-51 (—); vertebrae 49-51 (50).

PROPORTIONAL DIMENSIONS: Based on the neotype, SIO64-28, 1 (60.6) and 9 (42.5-103.5) additional specimens: LACM 7695, 1 (70.0); LACM 9078, 1 (60.0); LACM 9497, 1 (42.5); LACM 9628, 1 (87.0); LACM 9700, 1 (92.5); LACM 9806, 3 (46.1-103.5); LACM 30273, 1 (68.5). Expressed as thousandths of the S.L. and given as the mean, range (values in parentheses), and values for the neotype.

Body, depth at dorsal origin, 162 (129-190) 190. Caudal peduncle: least depth, 77 (66-84) 84; length, 101 (95-108) 102. Adipose fin: distance to midcaudal rays, 133 (124-143) 124; length of base, 41 (33-52); length of fin, 64 (52-75) 64. Anal fin: length of base, 251 (224-260) 249; length of longest ray, 105 (71-132) 132. Dorsal fin: length of base, 50 (44-57) 50; length of longest ray, 99 (82-115) 99; dorsal origin to anal origin (distance between verticals), 233 (212-251) 234; end of dorsal base to base of midcaudal rays, 520 (497-544) 497. Pectoral fin, length of longest ray, 207 (174-232) 213. Pelvic fin, length of longest ray, 197 (165-222) 216. Pelvic insertion to anal origin, 234 (191-253) 249. Pectoral insertion to pelvic insertion, 142 (149-162) 149. Anus to anal origin, 34 (24-50) 33. Distance from snout to: anus, 646 (617-678) 678; dorsal origin, 447 (431-474) 455; anal origin, 676 (638-713) 701; pectoral insertion, 301 (277-317) 317; pelvic insertion, 439 (416-467) 449; anterior margin of





eye, 81 (71-106) 83. Head length, 281 (259-318). Postorbital head length, 126 (118-132) 132. Eye: horizontal diameter, 70 (61-77) 76; vertical diameter, 65 (59-74) 74. Interorbital width, 32 (28-47) 35. Upper jaw length, 178 (164-191) 188. Lower jaw length, 199 (188-214) 206. Longest dentary tooth, 34 (31-41) 33.

BODY: Body depth 6.27 (5.26-7.74) 5.26 in S.L. Peduncle depth 3.67 (3.20-4.35) 3.50 in head length (H.L.) Peduncle length, 2.80 (2.61-3.00) 2.89 in H.L.

SKIN AND SCALES: Scales rows could not be counted in any available material. Lateral line scales relatively small, numbering 48-51 in six specimens counted. Lateral line scale above analorigin based on 2 (68.5-103.5) specimens and listed in that order: H/L 1.08-.940; T/L .470-.530; P/L .228-.260. Lateral line scale above pectoral insertion based on 1 (68.5) specimen: H/L 1.08; T/L .353; P/L .226. Penultimate and ultimate lateral line scales missing in all specimens examined, due to damage.

HEAD: Snout length exceeding eye diameter. Postorbital head depth and width subequal to body depth and width. Eyes tubular, directed dorsoanteriad. Pearl organ nearly elliptical with major axis normal to visual axis of eye. Head length 3.57 (3.15-3.86) 3.38 in S.L. Snout length 3.51 (3.00-3.74) 3.58 in H.L. Horizontal eye diameter, 4.06 (3.67-5.19) 3.89 in H.L. Postorbital head length 2.23 (2.11-2.41) 2.24 in H.L. Interorbital width 8.88 (6.75-9.85) 8.53 in H.L.

Head with densely pigmented areas on occiput, interorbital, snout, around orbit, and lining gape. A black band of pigment bordering anteroventral corner of eye. A dark spot between mandibles on midventral line anterior to union of gill membranes. Dense pigment medially on branchiostegal membranes.

Subopercle expanded, much larger than opercle. A shallow notch in subopercle opposite insertion of pectoral fin.

Pseudobranchiae well-developed, counts based on 4 (38.9, 60.6, 70.0, 92.5) specimens and listed in that order: 11, 16, 18, 18. Gill filaments moderately elongate but not reaching posterior border of gill covers.

MOUTH: Upper jaw length 1.58 (1.50-1.67) 1.56 in H.L. Lower jaw length 1.42 (1.33-1.50) 1.43 in H.L. Upper jaw terminating just behind a vertical through posterior margin of eye.

Tooth counts based on 5 (38.9, 60.6, 70.0, 92.5, 103.5) specimens and listed in that order. Premaxillary tooth counts: 24, 26, 37, 37, 41. Dentary tooth counts: lateral, 20, 22, 26, 28, 27; medial, 10, 5, 6, 8, 9. Palatine tooth counts: 6, 10, 11, 9, 12. Lingual teeth present over both basihyal and basibranchials. Lingual tooth counts: 11, 11, 9, 10, 7. Longest dentary tooth 8.26 (6.86-9.64) 8.95 in H.L.

FINS: Length of longest dorsal ray 9.9 (8.2-11.5) per cent S.L. Length of dorsal base 5.0 (4.4-5.7) per cent S.L. A short fleshy ridge extending anterior to adipose fin. Adipose to caudal distance distinctly less than in any other scopelarchid, 13.3 (12.4-14.3) 12.4 per cent S.L. Pelvic and pectoral fins subequal in length. Appressed pelvic fin reaching anal origin. Appressed pectoral fin reaching slightly past pelvic insertion.

COLOR: Color in alcohol a yellow-brown with the few remaining scale pockets edged in dense brown pigment. Two broad bands of dermal pigment, one extending from caudal peduncle to occiput dorsal to lateral line, the other ventral to lateral line, extending from caudal peduncle to just behind pelvics. The two dermal bands of pigment coalescing at caudal peduncle to form a dense bar of pigment anterior to bases of caudal rays. Dense pigment at bases of all fins, with pigment on rays and membranes of dorsal, pectoral, anterior half of anal, and dorsalmost and ventralmost caudal rays. Pigment lacking on pelvic rays and membranes. Peritoneum dense black.

Development.—The description of development in Rosenblattichthys volucris is based on 87 (5.9-39.0) larvae and metamorphosing specimens and 14 (40.5-70.0) adolescents and young adults. Figure 35 illustrates in sequence the development of this species.

RECOGNITION: Larvae of *R. volucris* can be distinguished through the following combination of characters: dorsal 9-10, anal 21-24, pectoral 23-26; head length in larvae up to 39 mm. exceeding 30 per cent S.L.; pectoral fins precocious, development of ossified pectoral rays greatly precedes development of dorsal, anal, or pelvic rays; one peritoneal section only; pelvic fins appearing as buds beneath or slightly behind vertical from middorsal base, about one-fourth of body depth from ventral contour of body; unique combination of up to seven pigment spots or areas (fig. 35), two middorsal spots, anterior spot over or slightly ahead of anal origin, posterior spot over midanal base; two caudal bars of pigment, above and below midcaudal rays; one pigment spot midlaterally on each side of caudal peduncle; two pigment areas on anal base, one on anterior fin ray bases, and one at bases of midanal rays; no pigment associated with ventroposterior margin of intestine.

FINS: In the smallest available specimen [SIO64-179, 1 (5.9)], dorsal four or five pectoral rays partially differentiated, remaining fins undifferentiated and median fins remain in fin-fold stage. Pectoral fins precocious, extremely prominent and elongate in early larvae. Pelvic fins appearing as buds about one-fourth of body depth from ventral contour of



body below or slightly behind vertical from last dorsal ray. Pelvic insertion in larger larvae beneath middorsal base or beneath anterior one-third of dorsal base. Ventral adipose fin never exceeds one-half pelvic-anal distance, and is reduced to a thin triangular flap in larvae 25-30 mm.in length. Dorsal adipose remains elongate, to over anal fin origin, in larvae as large as 30 mm., but is reduced to adult proportions in specimens larger than 40 mm. All fin rays ossified by 17-19 mm.S.L. Order of fin ray ossification: pectoral, caudal, dorsal, anal, pelvic.

PERITONEAL SECTIONS: Only one peritoneal section. Peritoneal section in smallest available larvae (5.9 mm. and larger), developing as thin, dark brown, transverse sheet above gut and medial to pectoral insertion. Peritoneum extends rearward during growth to form a canopy over gut, before expanding laterally to completely enclose gut in a tube of pigment.

ACCESSORY PIGMENT SPOTS OR AREAS: A maximum of seven accessory pigment spots or areas. Two middorsal accessory pigment areas, one (DAA) over or slightly ahead of vertical from anal origin, the second (DAP) centered over a vertical through middle of anal fin base and opposite PA. Two dash-like bars of pigment on caudal fin, one dorsal (CAD) and one ventral (CAV) to midcaudal rays. Two midlateral spots, one on each side, at center of caudal peduncle (PDA). Two pigment areas associated with bases of anal rays: one over anterior anal rays (AA) and one at midanal base (PA). There is no IA, a spot of pigment associated with posteroventral contour of gut, in R. volucris. In the smallest available larvae (5.9 mm.) only eye and peritoneal pigment is present. In the next smallest larvae [HMS 35-62, 1 (9.5); SIO64-179, 2 (10.5)] the following accessory pigment areas are developed: DAA, DAP, CAV, PA. In [S1068-618, 1 (11.1) (fig. 35)] all pigment areas but the AA are present. In [HMS 31-124, 1 (12.9)] and all larger larvae, all seven pigment areas are welldeveloped. Thus the order of appearance of accessory pigment areas appears to be as follows: DAA+DAP+CAV+PA; CAD; AA. With further growth, the CAD+CAV are eventually lost, the AA pigment spreads posteriorly over the bases of the anal rays and coalesces with the PA, while the remaining pigment areas are overgrown by skin.

DERMAL PIGMENTATION: Dermal pigmentation first appears in 28-30 mm. larvae. The first pigment to appear is that associated with the cranium, shielding the otherwise transparent cranial vault. Two body dermal pigment areas appear at middorsal contour nearly at the same time as the cranial pigment: one anteriorly over the pectoral insertion and one associated with the DAA. Dermal pigmentation is restricted to the body dorsal to the lateral line in larvae and metamorphosing speci-

mens less than 40 mm. The anterior pigment area spreads posteriorly eventually meeting the posterior pigment area which spreads both anteriorly and posteriorly, eventually resulting in even pigmentation above lateral line from occiput to procurrent caudal rays.

GUT: Post-pelvic gut length, about one-half pelvic-anal distance in smaller larvae, reaches maximum rearward extent in 35-40 mm. metamorphosing specimens. The complete enclosure of the gut by peritoneal pigment takes place by 40 mm. and larger specimens. Caecum visible in larvae less than 35 mm. as short dorsal protuberance from gut, not extending rearward of pectoral base. Caecum begins rearward expansion in 35-40 mm. larvae, but reaches maximum rearward extent, just before anus, in specimens 60 mm. and larger.

METAMORPHOSIS: R. volucris exhibits gradual metamorphosis, with changes in morphology leading from larval to adult form and pigmentation occurring over a fairly wide size range. These changes begin with the acquisition of dermal pigmentation in 28-30 mm. larvae. Larvae 30-40 mm, in size exhibit the following metamorphic changes: gradual overgrowth by skin of DAA, DAP, PDA; loss of CAD and CAV; rearward expansion of AA pigment area; loss of ventral adipose fin; reduction of dorsal adipose fin to adult dimensions; rearward expansion of peritoneal pigment and caecum; investiture of abdominal body wall with muscle tissue; continued expansion of epaxial dermal pigmentation. I have chosen the complete enclosure of the gut by a tube of peritoneal pigment as a somewhat arbitrary line of demarcation in terminology, specimens smaller than 40 mm. being called larvae and metamorphosing specimens, those larger than 40 mm. being termed adolescents and adults. Additional adult features acquired during the 40-50 mm. size range [based on LACM 9497, 1 (42.5); LACM 9806, 1 (46.1); ORSTOM Caride V-259, 1 (44.0); SIO50-277, 1 (41.5); SIO51-168, 1 (40.5); SIO64-29, 2 (41.1-47.2); SIO64-172, 1 (42.6); LACM 9806, I (50.0)] include the following: appearance of hypaxial dermal pigment midventrally on peduncle around and just behind last anal rays, as a patch ventral to lateral line over anterior anal rays, and as a series of melanophores arranged in a line parallel to anal base and slightly above it; appearance of pigment on head associated with interorbital region, snout, upper and lower jaws, and branchiostegal membranes; continuing rearward expansion of gut, peritoneal pigment, and caecum; and development of pigment on dorsal and anal fins. The smallest specimen I have seen with the pelvics inserted slightly ahead of a vertical from the dorsal origin is one 50.0 mm. (LACM 9806). All of these processes are complete in specimens 60 mm. and larger, and hence metamorphosis occurs over a size range of 28-60 mm.



FIG. 36. Distribution of *Rosenblattichthys volucris* (Rofen). Open symbols: records based solely on larvae. Closed symbols: records based on adults.

Distribution.—Rosenblattichthys volucris is restricted to the eastern half of the Pacific Ocean (fig. 36). In the eastern North Pacific it has been taken from the San Pedro Basin (33° 37.0-33.2' N) south to 25° 28.8-35.3' S, off Baja California, and offshore to 123° 56.0' W off Southern California. In the equatorial eastern Pacific *R. volucris* is limited to a narrow band along the equator from 140° W to the South American mainland between 6° N and 3° 12' S, thus occupying (with Scopelarchus guentheri, see below) the waters intervening between the two areas of distribution of Scopelarchoides nicholsi (see below). The following two outlying records are based on young individuals: (1) A single specimen 24.4 mm. S. L. taken at 10° 00-10' N, 161° 52.5-51.5' W, in August, 1968. (2) A single specimen 41 mm. S.L. questionably reported as Phanops volucris Rofen by Craddock and Mead (1970, p. 3.26) from 33° 20' S, 73° 42' W, off Chile. Although all other scopelarchid specimens recorded by Craddock and Mead were later made available to me for study, unfortunately this single specimen has apparently been lost.

R. volucris adults and larvae have been taken throughout the year, both off California and along the equator. Larvae have been taken at night in hauls to depths less than 100 m. Almost all hauls successfully capturing adults have been to depths greater than 400 m. by day and 300 m. by night.

Material examined.—A total of 108 (5.9-103.5) specimens from 71 collections. LACM: 6525, 2(23.1-32.5); 7530, 1(25.8); 7695, 1(70.0); 9016, 8(16.6-23.4); 9033, 2(28.5-29.2); 9034, 2(21.5-23.2); 9037, 2(29.0-32.6); 9058, 1(38.9); 9074, 1(31.5); 9078, 1(60.0); 9086, 2(22.5-24.0); 9087, 9(17.0-31.5); 9088, 1(28.8); 9092, 1(26.1); 9093, 1(31.0); 9497, 1(42.5); 9628, 1(87.0); 9636, 3(24.5-30.5); 9645, 1(23.1); 9671, 1(19.4); 9696, 1(18.0); 9700, 1(92.5); 9806, 3(46.1-103.5); 21311, 1(19.5); 30273, 1(68.5); 30280, 1(37.5). NMFS: HMS 31-121, 2(14.8-23.5); HMS 31-124, 1(12.9); HMS 31-146, 1(32.5); HMS 33-21, 1(29.5); HMS 35-62, 5 (9.5-15.5). ORSTOM: Caride V-259, 1(44.0). SIO: 50-277, 1(41.5); 50-290, 1(35.0); 50-70, 1(25.2); 51-168, 1(40.5); 52-404, 1(57.0); 55-244, 1 (ca. 31); 55-249, 2(20.5-23.5); 55-265, 1(16.0); 56-68, 1(26.5); 56-76, 1(33.0); 63-165, 1(26.1); 63-415, 1(36.7); 63-869, 1(39.0); 64-28, 1(60.6); 64-172, 1(42.6); 64-179, 3(5.0-10.1); 65-440, 1(32.2); 66-30, 1(27.2); 66-41, 1(17.0); 66-42, 1(34.5); 66-330, 1(26.0); 66-400, 2(22.2-23.0); 66-440, 1(20.0); 66-450, 1 (15.5); 66-356, 2(25.5-37.0); 66.546, 1(24.5); 66-553, 1(34.2); 66-597, 1(7.8); 67-49, 1(31.5); 68-536, 1(24.4); 68-582, 2(41.1-47.2); 68-618, 1(11.1); 70-19, 1(24.5); 70-21, 1(34.0); 70-240, 1(33.6). SIO uncat. 25° 44' N., 116° 01.5' W., 9 Nov. 56. 1 (36.0). SOSC: AB 16-619C, 1 (58.1); AB 16-622A, 1(46.5).

Scopelarchoides Parr 1929

Scopelarchoides Parr 1929, p. 14.

Type species.—Scopelarchoides nicholsi Parr 1929, p. 14.

Diagnosis.—Parietals present or absent, antorbital present, ethmoid process on first infraorbital present or absent, basihyal short or elongate, teeth restricted to basihyal or extending to over second or third basibranchial, suspensory pharyngobranchial present or absent, if absent, first epibranchial is supported on second pharyngobranchial, not at articulation between second epibranchial and second pharyngobranchial; coracoid expanded, coracocleithral fenestra small; 45-57 vertebrae; 46-59 lateral line scales; distinct stripes of dermal pigment present or absent; pelvic insertion in adults from slightly behind dorsal base to slightly ahead of dorsal origin; larvae with one or three peritoneal sections; accessory pigment spots present, middorsal and midventral spots entirely behind adipose and anal bases respectively; pelvic fin bud appearing midlaterally in abdominal cavity wall beneath or slightly behind dorsal base.

Description.—Frontals not greatly expanded, limited to anterior onethird of postorbital dorsal roof of skull; supraoccipital with spikelike







B



FIG. 37. Comparison of pigment patterns and larval morphology in *Scopelarchoides* species. A. S. signifer. S1070-121. 22.6 mm. B. S. climax. S1070-109, 18.6. C. S. danae. DANA 3948 1, 18.0. D. S. nicholsi. S1068-617, 24.5.

spine or with low bony ridge and short blunt knob; supramaxilla present; hyomandibular with four rodlike arms; two extrascapulars.

Dorsal 6-10, anal 20-29, pectoral 20-25, lateral line scales 46-59, vertebrae 45-57.

Body moderately to distinctly elongate, moderately to strongly compressed. Belly straight with low scaly ridge of skin between pelvics and anus. Luminous tissue probably present in *S. kreffti*. Lateral line scale above anal origin large in all, elongate and deep with moderately to extremely deep, alate tympanum, completely or partly covering large central pore. Largest body scales behind pectoral insertion. Dense stripes of dermal pigment present in *S. nicholsi, S. danae*, and *S. kreffti*, absent in *S. signifer* and *S. climax*.

LARVAE: Origin of pelvic fin buds in midlateral abdominal cavity wall beneath or behind dorsal base; one peritoneal section in *S. signifer*, and *S. climax* (larvae of *S. kreffti* are unknown), and three peritoneal sections, the posterior two paired and appearing above or in front of pelvic fin base, in *S. nicholsi* and *S. danae*. Accessory pigment spots present, middorsal (DA) and midventral (PA) spots entirely behind vertical through end of adipose and end of anal fin bases respectively (fig. 37). Metamorphosis gradual. Dorsal adipose remains elongate, to over anal origin in specimens to 30 mm in length, except *S. danae*.

KEY TO THE SPECIES OF Scopelarchoides (specimens 40 mm. and larger)

2(1). Pigment lacking on pectoral and pelvic fin rays and membranes; dermal pigment stripe ventral to lateral line area well-developed, little or no dermal pigment dorsal to lateral line (except on caudal peduncle); pectoral fin rays 23 or fewer; lateral line scales 52 or fewer.

Eastern Tropical Pacific.

Well-developed stripes of dermal pigment dorsal and ventral to lateral line (dorsal stripe more intensely developed than ventral stripe in adults); no pigment along dorsal margin of pearl organ; a dense black band of pigment along midventral line from just behind pectoral base to anus; internal pigment present around anal fin bases and radials; luminous organs probably present.S. kreffti Johnson 1972 South Atlantic.

KEY TO THE SPECIES OF Scopelarchoides:

LARVAL AND METAMORPHIC SPECIMENS (specimens 7 mm. and larger)

1.	Dorsal accessory spot present immediately behind dorsal adipose base (DA) 2
	Dorsal accessory spot absent
2(1).	Two accessory pigment spots only, DA and PA (fig. 37); one peritoneal section only; no 1A or CA
	A maximum of four accessory pigment spots, DA and PA, as well as a spot at fork of caudal fin (CA) and a spot on intestine near anus (IA); three peritoneal sections in specimens 17 mm. and larger
3(1).	One accessory spot only, PA, immediately behind last anal ray (Fig. 37); one peri- toneal section only, appearing beneath dorsal base
	A maximum of three accessory pigment spots, PA present, IA present on gut, and PDA spots present midlaterally on each side of caudal peduncle; three peritoneal sections in larvae 26-28 mm. and larger
	Larvae of S. kreffti are unknown.

Scopelarchoides climax Johnson 1974. Figure 38.

Scopelarchoides climax Johnson, 1974, p. 453.

Holotype.—99.3 mm. S.L. Central South Pacific. SIO70-107. 24° 56.1-25° 05.1′ S, 154° 59.9-155° 03.9′ W, (IKMT: 3500 mwo), October 4, 1969.

Comparative diagnosis.—A species of *Scopelarchoides* with 7-8 dorsal rays, 25-27 anal rays, 25 pectoral rays, and 53 (based on one specimen) lateral line scales; pelvic fins much longer than pectoral fins and inserted under first dorsal ray; no enlarged midventral pigment areas; dense pigment at bases of paired fins and light pigment on rays and membranes; a cap of enlarged black melanophores dorsal to pearl organ. The combination of these characters distinguishes *Scopelarchoides climax* from all other known species of scopelarchids.



Description.—Based on 4 (18.6-21.8) larvae, 3 (33.5-36.5) adolescent specimens, and 1 (99.3) adult. With the exception of meristic characters and where otherwise noted, the description given below is based solely on the holotype, and is followed by an account of the known larval and adolescent specimens.

MERISTIC CHARACTERS: Values for the holotype are listed in parentheses. Dorsal 7-8 (8); anal 25-27 (25); pectoral 25 (all); lateral line scales (53); vertebrae 49 (based only on holotype).

PROPORTIONAL DIMENSIONS: Based on the holotype and 3 adolescent specimens (33.5, 35.5, 36.5) and listed in that order. Only selected measurements (for purposes of comparison with *Scopelarchoides kreffti*) were taken from the adolescents, single values listed below are those of the holotype.

Body, depth at dorsal origin, 147, 134, 120, 112. Caudal peduncle: least depth, 76, 67, 60, 66; length, 130, 112, 120, 123. Adipose fin: distance to midcaudal rays, 227, 213, 197, 216; length of base, 41; length of fin, 76. Anal fin: length of base, 297, 310, 292, 329; length of longest ray, 107. Dorsal fin: length of base, 41; length of longest ray, 86; dorsal origin to anal origin (distance between verticals), 247; end of dorsal base to base of midcaudal rays, 599, 630, 594, 616. Pectoral fin, length of longest ray, 132. Pelvic fin, length of longest ray, 173. Pelvic insertion to anal origin, 280. Pectoral insertion to pelvic insertion, 162. Anus to anal origin, 40. Distance from snout to: anus, 613; dorsal origin, 369, 370, 352, 381; anal origin, 661, 555, 589, 562; pectoral insertion, 257, 257, 246, 249; pelvic insertion, 403; orbit, 72, 90, 85, 88. Head length, 227, 242, 225, 247. Postorbital head length, 65, 78, 74, 71. Orbit: horizontal diameter, 91, 67, 63, 85; vertical diameter, 87. Interorbital width, 13. Upper jaw length, 171, 168, 144, 164. Lower jaw length, 196, 193, 165, 192. Longest dentary tooth, 21.

BODY: Body moderately elongate, shallow, strongly compressed. Belly straight with a low, scaly ridge of skin at midventral line between pelvics and anus. Body depth 6.80 in S.L. Peduncle depth 3.00 in H.L. Peduncle length 1.74 in H.L.

SKIN AND SCALES: Largest body scale ventroposteriad to pectoral base, truncate anteriorly, with large central focus, circuli more numerous and more closely spaced anteriorly. About five series of body scales from lateral line to dorsal origin and about eight series from lateral line to anal origin. About 38 series of scales from occiput to dorsal origin and about 65 series from dorsal origin to adipose origin. Body scales in vicinity of lateral line much smaller than lateral line scales. Lateral line scales large, numbering 53 in holotype. Lateral line scale above anal origin: height/length, 1.52; tympanum height/length, 1.08; pore height/length, .322; tympanum rounded anteriorly, not indented, extremely alate, completely covering large central pore. Lateral line scale above pectoral insertion: height/length, 1.27; tympanum height/length, .865; pore height/length, .344; tympanum similar to that of anal lateral line scale. Penultimate lateral line scale: height/length, 1.71; tympanum height/length, 1.38; pore height/length, .361. Ultimate lateral line scale: height/length, .701; imperforate, circuli incomplete, no posterior field, reaching to base of midcaudal rays.

HEAD: Dorsal profile rounded, descending moderately to rounded snout. Snout length less than horizontal eye diameter. Head depth and width subequal to body depth and width. Pearl organ capped dorsally by a band of enlarged jet-black melanophores. Head length 4.41 in S.L. Snout length 3.17 in H.L. Horizontal eye diameter 2.50 in H.L. Postorbital head length 3.47 in H.L. Interorbital width 17.30 in H.L.

Head densely pigmented, with especially dark pigmentation on occiput, interorbital region, orbit, and snout, and less dense on cheeks, gill covers, and jaws.

Subopercle larger than opercle. Opercle rounded posteriorly. Pectoral insertion opposite a notch at opercle-subopercle border.

Pseudobranchiae well-developed. Counts: 13. Gill filaments relatively short, not reaching edge of gill covers. Gill membranes united under posterior one-third of eye.

MOUTH: Upper jaw length 1.32 in H.L. Lower jaw length 1.15 in H.L. Upper jaw terminating under posterior one-third of eye. Premaxillary tooth count: 63. Dentary tooth counts: lateral 22, medial 15. Longest dentary tooth 10.70 in H.L. Palatine teeth arranged in two irregular rows with four large lanceolate fangs medial to nine smaller lateral teeth. Lingual teeth essentially limited to elongate basihyal with only two small teeth over anterior end of first basibranchial. Count: 11. Lingual teeth larger anteriorly but more strongly hooked posteriorly.

FINS: Dorsal moderately long, length of longest dorsal ray 8.6 per cent S.L.; length of dorsal base 4.1 per cent S.L. Dorsal origin well before midlength. Pelvics inserted under first dorsal ray, distinctly longer than pectoral fins. Length of longest pelvic ray ca. 17.3 per cent S.L.; length of longest pectoral ray 13.2 per cent S.L. Both pelvics and pectorals are somewhat frayed in holotype, but appressed pelvics probably do not reach anus while appressed pectorals reach just beyond pelvic insertion. Anal elongate, anal base 29.7 per cent S.L. Anal origin far behind midlength, preanal distance 66.1 per cent S.L.

COLOR: Body rather uniformly pigmented. In alcohol, body basically brown with dense pigment outlining scale pockets. All fin membranes lightly pigmented and dense pigment is present at bases of all fins.

Development.—The description of development in *Scopelarchoides climax* is based on 4 (18.6, 19.9, 20.0, 21.8) larvae and 3 (33.5, 35.5, 36.5) adolescent specimens. Figure 38 illustrates a larval and an adolescent specimen.

RECOGNITION: Larvae of *S. climax* can be distinguished by the following combination of characters: dorsal 7-8, anal 25-27, pectoral 25; one peritoneal section only, appearing dorsal to pelvic fin base in extreme dorsal part of abdominal cavity, and expanding anteriad and posteriad with growth; one accessory pigment spot, immediately behind last anal ray in midventral caudal peduncle (PA); no DA, PDA, or IA; pigment spots present on pectoral fin.

BODY: Body short, deep, with moderately deep peduncle. Head length relatively large, 28.4-32.0 per cent S.L. in 4 (18.6-21.8) larvae, 22.5-24.7 per cent S.L. in 3 (33.5-36.5) adolescents.

FINS: Pelvic and lower portion of pectoral fin rays non-ossified in three smaller larvae. Pelvic rays ossified but not lower three or four pectoral rays in 21.8 mm. larva. Pelvic fins in larvae inserted well behind last dorsal ray, pelvic fins inserted beneath middle of dorsal base in adolescents, and under first dorsal ray in holotype. Pelvic fins lie above or lateral to gut in larvae, and at ventrolateral body margin in adolescents. Ventral adipose fin about one-fourth of pelvic to anal distance in larvae, almost completely reabsorbed in adolescents. Dorsal adipose elongate in both larvae and adolescents, extending anterior to vertical through anal origin in larvae, and to anterior one-third of anal base in adolescents.

PERITONEAL SECTIONS: Only one peritoneal section, appearing above pelvic fin base at middorsal limit of abdominal cavity, forming a flattened sheet of pigment which expands anteriad and posteriad with growth. In adolescent specimens peritoneum has expanded to adult proportions and has nearly fused ventrally. Complete tube of peritoneal pigment around gut present in holotype.

ACCESSORY PIGMENT SPOTS: Only one accessory spot, PA, on ventral midline of caudal peduncle immediately behind last anal ray. PA evident in all larval and adolescent specimens but not in holotype and thus probably lost with growth.

DERMAL PIGMENTATION: Apparently absent in this species.

GUT: Post-pelvic gut length in larvae about three-fourths of pelvic-anal distance. Gut near anus lies outside of main portion of abdominal cavity and is supported by a thin flap of skin continuous with ventral adipose fin. Gut entirely within abdominal cavity in adolescents. Caecum not evident in larvae but reaches nearly to anus in adolescents. METAMORPHOSIS: The course of metamorphosis is incompletely known in this species. The 3 (33.5-36.5) adolescent specimens have not completed metamorphosis, defined by the complete enclosure of the gut by peritoneal pigment.

Distribution.—Scopelarchoides climax is known only from the central South Pacific between 24.5 and 25° S and around 155° W, near the Tubuai Islands. This area is near the western edge of the Eastern South Pacific Central Water mass (Sverdrup et al., 1942, p. 701). The known distribution of S. climax is shown in Figure 41.

The holotype and all but three paratypes were taken with an IKMT with 3500 mwo. Three paratypes were taken with an IKMT fitted with 505μ plankton mesh, 2(20.0-35.5) taken with 700 mwo, and 1(19.9) taken on a haul between 0-175 m., suggesting that the larvae of this species occur above the thermocline. Eight of the nine known specimens were captured with five days of each other, October 3-8, 1969.

Material examined.—A total of 9 (18.6-99.3) specimens from seven collections. **S10: 70-**107.1 (99.3); 70-109, 1 (18.6); 70-110, 1 (33.5); 70-112, 2 (21.8-36.5); 70-118, 1 (19.9); 70-121, 2 (20.0-35.5); 72-311, 1 (18.5).

Scopelarchoides danae Johnson 1974. Figure 39.

Scopelarchoides danae Johnson 1974, pp. 453-454.

Holotype.—96.4 mm. S.L. South China Sea. SIO70-341. 18° 14.4-05.5′ N, 119° 45.2-24.8′ E, (IKMT: 0-1850 m.), September 17, 1970.

Comparative diagnosis.—A species of Scopelarchoides with 6-9 (usually 7 or 8) dorsal rays, 24-27 anal rays, 20-22 pectoral rays, and 50-52 lateral line scales; pelvic fins distinctly longer than pectoral fins; origin of pelvic fins under anterior one-third of dorsal base; heavy dermal pigmentation forming a stripe just ventral to lateral line but dermal pigment absent or weakly developed dorsal to lateral line; heavy pigmentation on ventral lobe of caudal fin but pigment absent or very weakly developed on dorsal lobe of caudal fin. The combination of these characters distinguishes Scopelarchoides danae from all other known species of scopelarchoids.

Description.—Based on 154 (6.5-49.7) larval and metamorphic specimens and 45 (51.5-121.5) adolescent and adult specimens. With the exception of meristic characters, the description based upon adults is given first followed by an account of development.

MERISTIC CHARACTERS: Values in parenthesis are those of the holotype. Dorsal 6-9 (57/61 had dorsal = 7 or 8) (8); anal 24-27 (26); pectoral 20-22 (21); lateral line scales 50-52 (51); vertebrae 48-50 (49).

PROPORTIONAL DIMENSIONS: Based on 22 (39.0-111.0) specimens:





North Atlantic: DANA 1181 V, 2 (81.2-111.0); DANA 1215 V, 1 (80.1); USNM, ACRE 7-17, 1 (69.3); WHOI, RHB 1250, 1 (45.0); RHB 1258, 2 (64.1-66.0); RHB 1267, 1 (53.9); RHB 1302, 1 (65.0); RHB 1313, 1 (69.6). Indian Ocean: DANA 3830 V, 1 (92.0); DANA 3906 III, 1 (53.5); DANA 3949 1, 1 (71.7). Western Pacific: DANA 3687 11, 3 (39.0-69.6); DANA 3734 II, 1 (104.5); DANA 3744 I, 1 (68.0); DANA 3789 VII, 1 (67.8); DANA 3797 11, 1 (56.5); SIO61-584, 1 (89.1); SIO70-341, 1 (96.4) holotype. Expressed as thousandths of the standard length and given as the mean, range (in brackets), and the values for the holotype (in parentheses). Body, depth at dorsal origin, 136[109-162](157). Caudal peduncle: least depth, 75 [63-81] (78); length, 128 [113-147] (130). Adipose fin: distance to midcaudal rays, 164 [150-178] (171); length of base, 34 [23-39] (36); length of fin, 64 [55-76] (57). Anal fin: length of base, 317 [301-334] (307); length of longest ray, 115[95-140](140), Dorsal fin: length of base, 38[32-44](32); length of longest ray, 64 [47-88] (88); dorsal origin to anal origin (distance between verticals), 194 [181-208] (202); end of dorsal base to base of midcaudal rays, 601 [589-615] (591). Pectoral fin, length of longest ray, 136 [89-155] (147). Pelvic fin, length of longest ray, 171 [133-205] (205). Pelvic insertion to anal origin, 178 [152-210] (182). Pectoral insertion to pelvic insertion, 180 [166-202] (176). Anus to anal origin, 55 [38-68] (48). Distance from snout to: anus, 530 [508-583] (545); dorsal origin, 377 [358-400] (390); anal origin, 579 [558-640] (579); pectoral insertion, 226[211-252] (228); pelvic insertion, 400 [377-428] (406); orbit, 61[53-71] (63). Head length, 204 [189-218] (206). Postor bital head length, 87 [78-93] (78). Orbit: horizontal diameter, 60 [47-78] (63); vertical diameter, 57 [50-72] (62). Interorbital width, 20 [11-36] (15). Upper jaw length, 144 [133-158] (146). Lower jaw length, 163 [154-181] (170). Longest dentary tooth, 32[27-40] (36).

BODY: Body elongate, deep, strongly compressed. Body depth 7.45 [6.18-9.19] (6.38) in S.L. Peduncle depth 2.71 [2.46-2.97] (2.65) in H.L. Peduncle length 1.59 [1.44-1.82] (1.59) in H.L.

SKIN AND SCALES: Body and head scales, and scale pockets absent in all specimens examined, probably due to damage caused by capture. Lateral line scales large, numbering 50-52 in 37 specimens counted. Lateral line scale above anal origin based on 18 [North Atlantic, 8 (37.5-114.6); Indian 2 (92.0-121.2); Western Pacific, 7 (65.2-104.5); Central Equatorial Pacific, 1 (86.1)] specimens: height/length, 1.32 [1.21-1.48] (1.28); tympanum height/length, .860 [.610-1.160] (.885); pore height/length, .308 [.268-.390] (.310); tympanum large, alate, rounded at anterior margin, completely covering large central pore. Lateral line scale above pectoral insertion, based on 3 specimens [Central Equatorial Pacific, 1 (86.1); Indian, 1 (92.0); Western Pacific, 1 (104.5)] and listed in that order: height/length, 1.26, 1.20, 1.08; tympanum height/ length, .830, .730, .678; pore height/length, .343, .282, .245; tympanum smoothly rounded anteriorly. Penultimate lateral line scale, based on 4 specimens [Central Equatorial Pacific, 1 (86.1); Indian, 1 (92.0); Western Pacific, 2 (96.4-104.5)] and listed in that order: height/length, 1.90, 2.04, 2.04; 2.04; tympanum height/length, 1.18, 1.29, 1.21, 1.38; pore height/length, .338, .377, .334, .383. Ultimate lateral line scale, based on 2 [Central Equatorial Pacific, 1 (86.1); Western Pacific, 1 (96.4)] specimens and listed in that order: height/length, 1.48, 1.48; imperforate, circuli incomplete, no posterior field, reaching nearly to base of midcaudal rays.

HEAD: Dorsal profile straight, nearly horizontal with slight downward slope from occiput to snout. Eye diameter and snout length subequal. Head depth slightly less than body depth. Head width and body width subequal. Head length 4.92 [4.29-5.30] (4.85) in S.L. Snout length 3.35 [2.97-3.68] (3.26) in H.L. Horizontal eye diameter 3.45 [2.82-4.22] (3.26) in H.L. Postorbital head length 2.35 [2.12-2.69] (2.65) in H.L. Interorbital width 11.10 [5.78-17.60] (14.20) in H.L.

Occiput, dorsoposterior corner of orbit, interorbital area, snout, anterior and lateral surface of premaxillary; anterior, lateral and anteroventral surface of mandible densely pigmented. A layer of guanine beneath first and second infraorbitals. A dense streak of pigment bordering anterior margin of eye.

Opercle equal to or slightly deeper than subopercle; posterior margin of opercle weakly serrate. Pectoral insertion opposite a weak notch in gill cover at opercle-subopercle border.

Pseudobranchiae well-developed. Counts: (80.0) 10; (96.4) 11. Gill filaments not extending to edge of gill covers. Gill membranes united slightly anterior to vertical through anterior margin of eye.

MOUTH: Upper jaw length 1.41 [1.36-1.50] (1.41) in H.L. Lower jaw length 1.25 [1.18-1.35] (1.21) in H.L. Upper jaw terminating near articulation of lower jaw, well posterior to posterior border of eye.

Tooth counts based on 4 (45.0, 68.1, 89.1, 114.6) specimens and listed in that order. Premaxillary tooth counts: 30, 40, 55, 69. Dentary tooth counts: lateral, 17, 20, 25, 39; medial, 6, 6, 8, 8. Longest dentary tooth 6.42 [5.43-7.35] (5.69) in H.L. Palatine tooth counts: 8, 11, 10, 13. Lingual teeth on both basihyal and over first two basibranchials, counts: 8, 14, 11, 16.

FINS: Dorsal relatively short, length of longest dorsal ray 6.4 [4.7-8.8] per cent S.L.; length of dorsal base 3.8 [3.2-4.4] per cent S.L. Pelvics inserted under anterior one-third of dorsal fin base. Appressed pelvic fins reach to or slightly beyond anal origin. Pelvic rays noticeably stouter and longer than pectoral rays. Length of longest pelvic ray 17.1 [13.3-20.5] per cent S.L.; length of longest pectoral ray 13.6 [8.9-15.5] per cent S.L. Appressed pectoral fins reach to or slightly beyond pelvic insertion in best preserved specimens. Anal base moderately elongate, 31.7 [30.1-33.4] per cent S.L. Anal origin well behind midlength, preanal distance 57.9 [55.8-64.0] per cent S.L.

COLOR. Dermal pigmentation on body essentially confined to a marked stripe bordering ventral margin of lateral line from over pelvic base to caudal peduncle, increasing slightly in depth from anterior to posterior and essentially covering posterior portion of peduncle. Dermal pigment absent or very weakly developed dorsal to lateral line except on caudal peduncle. Scale pockets edged with pigment only dorsal to lateral line. Scaly flaps of skin overlying bases of caudal rays well-pigmented. Pigment lacking on pectoral, pelvic, anal, and adipose fins. Pigment weakly developed at bases and part of length of first four or five dorsal rays. Pigment strikingly well developed along entire ventral lobe of caudal fin, but lacking or much less well-developed on dorsal lobe of caudal fin.

Development.—The description of development in Scopelarchoides danae is based on 154 (6.5-49.7) larval and metamorphic specimens and 26 (51.5-69.6) adolescent and young adult specimens. Figure 40 illustrates in sequence the development of this species.

RECOGNITION: Larvae of *S. danae* can be distinguished through the following combination of characters: dorsal 6-9 (usually 7-8); anal 24-27; pectoral 20-22; one peritoneal section in larvae 16 mm or less, situated in anterior portion of abdominal cavity dorsomedial to gut; three peritoneal sections in larvae larger than 16 mm, one anterior and two paired posterior sections appearing above pelvic base, the rear sections expanding rapidly with growth anteriad and posteriad; unique combination of four accessory pigment spots, one midventral in caudal peduncle immediately behind last anal ray (PA), one middorsal in caudal peduncle, positioned slightly in advance of vertical through PA and situated close behind adipose fin base (DA); a slash-like bar of pigment on caudal fin, situated at middle of caudal fin just behind bases of midcaudal rays (CA); a pigment spot in midventral wall of intestine, just anterior to anus (IA); no PDA.

BODY: Body elongate, relatively shallow, with moderately deep ped uncle. Head relatively small, less than one-fourth of standard length in larvae up to 25 mm., around one-fifth of standard length in specimens larger than 25 mm.



FINS: No ossified rays in smallest (6.5-9.0) larvae. Notochord flexure occurs in larvae 8-10 mm. Caudal rays ossified in larvae 10-11 mm. and larger. All fin rays ossified in specimens 19 mm and larger. Apparent order of ossification: caudal, anal, dorsal, dorsal pectoral, pelvic, ventral pectoral. Pelvic fins appear as buds beneath middle of dorsal base in midlateral abdominal cavity wall, well above level of intestine. Pelvic fins at ventral contour of body, as in adults, in specimens 16-17 mm. and larger. Pelvic insertion in specimens 20 mm. and larger under anterior one-third of dorsal base. Ventral adipose fin two-thirds of pelvic-anal distance in smaller larvae, reduced to a thin flap in specimens 16-22 mm., and lost in specimens 23-24 mm. and larger. Dorsal adipose extends to over anterior one-third of anal base or further anteriad in specimens 16 mm. and smaller, and is reduced to essentially adult proportions in specimens larger than 20 mm.

PERITONEAL SECTIONS: A single peritoneal section in larvae less than 16 mm, situated in anterior portion of abdominal cavity dorsomedial to gut. Anterior peritoneal section present as a simple transverse sheet in smallest (6.5) larva, and expands to form two lateral wings connected dorsally and enclosing gut dorsally, but does not expand posteriad to any great extent at any time during growth. Two paired peritoneal sections first appear in a 16.1 mm. larva as a small dash of pigment in midlateral abdominal cavity wall above pelvic fin base. Paired sections expand rapidly both anteriad and posteriad with growth, reaching almost to anterior single section and to anal origin in specimens 20 mm, and larger. A long delay between longitudinal and ventrolateral expansion occurs, and the peritoneal sections are not joined anteriorly or fused ventrally in specimens less than 45 mm. in size. Fusion between anterior single and posterior paired sections occurs along a line about one-third of distance from pectoral insertion to pelvic insertion behind pectoral insertion. First formation of complete tube around gut occurs in posterior portion of paired sections which are fused dorsally and ventrally in specimens 40-45 mm. and larger.

ACCESSORY PIGMENT SPOTS: Four accessory pigment spots. A midventral spot (PA) on caudal peduncle immediately behind last anal ray. A middorsal spot (DA) on caudal peduncle just behind adipose base and located slightly forward of a vertical through PA. A slash-like bar of pigment (CA) at fork of caudal fin just posterior to bases of midcaudal rays. An intestinal spot (1A) set in midventral intestinal wall just anterior to anus. No PDA.

DA, PA, and CA present in smallest larva (6.5 mm.). CA appears as spot ventral to notochord tip in larvae that have not undergone notochord flexion, and is found on midcaudal area after notochord flexion. In my material an IA present only in larvae 10.1-33.9 mm. in size, apparently lost or becoming indistinguishable in larger specimens. DA, PA, and CA overgrown by skin and muscle tissue in larger specimens, but present in adults.

DERMAL PIGMENTATION: Appearance of dermal pigmentation occurs slightly after appearance of paired peritoneal sections. Dermal pigment on body in specimens 20 mm. and larger. Dermal pigment first appears on caudal peduncle and ventral to lateral line, and expands anteriad forming an hypaxial stripe similar to adults in specimens 30 mm. and larger. Formation of pigment on ventral caudal lobe begins in 45-50 mm. specimens and is similar to that of adults in specimens 55 mm. and larger. Head pigment first appears as line of pigment edging dentigerous area of mandible. Additional pigment appears on occiput, around nostrils, and along premaxillary. Pigment similar to adults in specimens 60 mm. and larger.

GUT: Post-pelvic gut length in smallest larvae about one-third pelvicanal distance, increasing during growth and reaching essentially adult proportions in specimens 20-23 mm. and larger. Caecum begins to expand in 20-23 mm. specimens, reaching nearly to anus in specimens 45 mm. and larger.

METAMORPHOSIS: Metamorphosis gradual, beginning with appearance of paired peritoneal sections in 16-17 mm. specimens and completed with fusion of peritoneal sections and maximum rearward extension of caecum in specimens 50 mm. and larger. Investiture of abdominal cavity wall with muscle, maximum caecum expansion, and fusion of peritoneal sections occurs in specimens 45-55 mm. in size, thus 50 mm. taken as somewhat arbitrary endpoint of metamorphosis.

Distribution.—Scopelarchoides danae is a wide-ranging centraltropical species occurring in all three oceans (fig. 41). S. danae has been taken on both the eastern and western sides of the North Atlantic as well as in the Caribbean Sea, Gulf of Mexico, and Gulf of Guinea. S. danae is not yet known from the South Atlantic, but its presence at the equator in the Gulf of Guinea and to 26° S, off the east coast of South Africa, as well as the lack of any apparent differences between North Atlantic specimens and those from elsewhere suggests that S. danae will be taken in the South Atlantic. S. danae occurs throughout the Indian Ocean from 26° S off southern Africa to ca. 6° N off Sumatra. S. danae occurs throughout the South China Sea and the semi-isolated seas of the Indo-Malayan Archipelago. S. danae is known from but two adult specimens in the Pacific, both specimens taken near islands: one (113.6) taken near New Caledonia (22° 03.0' S, 165° 58.0' E, 0-560 m.) the





other, one (86.1) near the Marquesas (09° 54' S, 141° 33' W, 0-900 m.). S. danae has not been taken, and probably does not occur, in the central portions of the central gyrals of the Pacific away from island chains, nor does it occur in the eastern Pacific. The distribution of S. danae is similar in many respects to that of R. alatus (see above) and S. signifer (see below), although the latter are not known from the Atlantic Ocean. It is somewhat surprising that S. danae has not been captured in nearshore waters around Hawaii nor in the Climax Expedition station near 24.5° S, 155° W near the Tubuai Archipelago.

Larvae of *S. danae* have been taken throughout the year. Larvae have been taken in numerous hauls to less than 100 m. in depth. Adolescent specimens (50-70 mm.) have been captured on numerous occasions in hauls 100-200 m. in depth, and on one occasion [AB 8-405 A] in a plankton tow 0-70 m. (1 specimen, 52.3 mm.). Adults (larger than 70 mm.) have been captured in numerous night-time tows to 300-500 m. in depth, but are known from a total of four daytime tows, all to depths in excess of 500 m.

Material examined.—A total of 200 (6.5-121.2) specimens from 80 collections.

North Atlantic. CAS: 14300, 1 (109); DANA: 1180I, 2 (38.9-47.6); 1181V, 2 (81.2-111.0); 1182II, 3 (30.1-51.5); 1185I, 1 (49.7); 1215V, 1 (80.1); 1223II, 1 (15.0); 1269VIII, 2 (37.5-54.0); 12821, 1 (101.6); 12841, 1 (114.6); 12851, 1 (110.5); 12871, 1 (44.3); 1291V, 1 (17.0); 1296111, 6 (26.5-33.4); 40011, 1 (93.4); 40011V, 30 (12.5-26.1); ISH 2285/71, 1 (115.0); LACM: *Thierry*, Guinean Trawling Survey II, Transect 51, Sta. 8, 1 (101.0); SIO: 63-560, 1 (16.1); 70-364, 1 (14.0); USNM: ACRE: 4-13B, 1 (29.5); 7-17, 1 (69.3); WHOI: RHB: 1100, 1 (22.1); 1250, 4 (43.1-45.0); 1258, 4 (57.5-66.0); 1261, 3 (31.1-68.1); 1264, 4 (30.9-62.0); 1267, 1 (53.9); 1268, 1 (25.2); 1273, 6 (10.2-18.1); 1277, 6 (19.8-33.9), 1302, 1 (65.0); 1313, 1 (69.6).

Indian Ocean. DANA: 3804111, 2 (14.6-17.6); 38041V, 2 (11.6-12.0); 3828 V11, 2 (117.7-121.2); 3830V, 1 (92.0); 388811, 1 (20.5); 390211, 1 (43.0); 3906111, 4 (23.0-53.5); 392711, 1 (6.5); 3929V11, 1 (20.0); 39311V, 1 (8.8); 3943111, 4 (12.2-23.0); 394411, 10 (7.5-12.1); 3944111, 10 (9.0-15.5); 3946111, 2 (18.6-23.0); 39481, 3 (9.7-18.0); 3948111, 1 (10.0); 39491, 1 (71.7); 39491V, 2 (18.5-19.0); 39501, 3 (7.0-8.6); 39511, 3 (10.0-13.5); 3951111, 7 (7.1-15.1); 39531, 4 (7.1-11.5); 39551, 2 (16.1-21.5); 395511, 4 (8.0-18.1); 39621V, 1 (12.6); 396411, 2 (27.0-37.0); 3964111, 5 (7.1-14.0); SIO: 61-33, 1 (78.8); 69-28, 1 (63.2); SOSC: AB 8-404A. 1 (52.3); TV 5-186, 1 (ca. 55).

Western Pacific. DANA: 368711, 3 (39.0-69.6); 373411, 1 (104.5); 3744 1, 1 (68.0); 3789 V11, 1 (67.8); 3797 11, 1 (56.5). ORSTOM: Coriolis p 1-6, 1 (113.6). SIO: 61-546, 1 (17.5); 61-578, 1 (65.2); 61-579, 1 (65.1); 61-584, 1 (89.1); 61-588, 1 (18.0); 61-639, 3 (12.5-27.6); 61-650, 1 (65.4); 61-706, 2 (17.5-23.0); 61-713, 1 (69.2); 69-20, 1 (63.3).

Central equatorial Pacific. ORSTOM: Caride V - 20A, 1 (86.1). **DANA:** 3567 1, 1 (17.4). **SIO:** 70-341, 1 (96.4).

Scopelarchoides kreffti Johnson 1972. Figure 42.

Scopelarchoides kreffti Johnson 1972, pp. 37-42.


Holotype.—ISH 1561. 159.0 mm. S.L. Western South Atlantic, 34° 01'S, 47° 39' W. (CMBT: 0-2000 m.). February 14, 1968.

Comparative diagnosis.—A species of Scopelarchoides with 9 dorsal rays, 25-27 anal rays, 23-25 pectoral rays, 58-59 lateral line scales, and 55-57 vertebrae. Pelvic fins considerably longer than pectoral fins and in adults inserted slightly in advance of dorsal origin. Both pectoral and pelvic fins densely pigmented. No cap of enlarged melanophores on dorsal margin of pearl organ, but lines of dark pigment present upon anterior and posterior margins of eye. Dense band of black pigment, unique to this species, present upon midventral line from just behind pectoral base to anus. Organs of *Benthalbella infans* present and probably luminous. The combination of these characters distinguishes *S. kreffti* from all other known scopelarchids.

No new material of *S. kreffti* has come to hand and the description of this species is not repeated here.

Comments on development.—Larvae of S. kreffti remain unknown. I have provided below an expanded description of the 8 (52.6-68.0) juvenile paratypes.

In the smallest (52.6) available specimens of *S. kreffti*, only a single peritoneal section is evident, enclosing the gut dorsally and laterally but incomplete ventrally. A black sheath of pigment partially encloses the AO organ and the anus which are situated immediately anterior to the anal fin origin. I was unable to determine whether this AO pigmented sheath is in fact peritoneal pigmentation, and knowledge of the origin of this sheath and its development relative to the abdominal cavity awaits the availability of larval material of *S. kreffti*. In larger juveniles and adults the AO sheath and the peritoneal section (which expands posteriad with growth) cannot be distinguished in gross dissection.

No accessory pigment spots or areas are apparent in the juveniles of *S. kreffti.* If larvae lack accessory pigment spots or areas, this would be a character state unique to this species among the species of *Scopelarchoides.*

Dermal pigmentation in the juveniles is essentially as in the adults although less developed, except that the stripe of dermal pigmentation ventral to the lateral line is markedly more developed in the juveniles, that dorsal to the lateral line is more strongly developed in adults (fig. 42).

Pigment lacking on the paired and anal fins in the juveniles but is present at the bases of the dorsal and caudal fins. The posterior end of caecum lies just behind the pelvic base in the smallest juveniles and halfway from the pelvic insertion to the anal fin in the largest juveniles. Distribution.—S. kreffti is known from a total of five hauls in the western and central South Atlantic between 34-41° S, 48-07° W (fig. 41). All specimens were taken with the CMBT 1600 Trawl employed in cruises of the FFS Walther Herwig. S. kreffti is apparently a member of a distinctive Subtropical Convergence Fauna discussed by Gibbs (1968).

Material examined.—A total of 10 (52.8-187.5) specimens from five collections, including the holotype and nine paratypes. **ISH** 630/71, 1 (187.5); ISH 649/71, 6 (56.5-68.0); ISH 666/71, 1 (52.6); ISH 1012/71, 1 (60.3); ISH 1561/68, 1 (159.0).

Scopelarchoides nicholsi Parr 1929. Figure 43.

Scopelarchoides nicholsi Parr, 1929, pp. 14-17; 1931, pp. 35-37; Mead and Böhlke, 1953, p. 244; King and Iverson, 1962, p. 320; Rofen, 1966e, p. 573.

Scopelarchus nicholsi Marshall, 1955, p. 314; Ebeling, 1962, p. 141; Bussing, 1965, p. 211; Berry and Perkins, 1966, p. 667; Lavenberg and Fitch, 1966, p. 104; Weitzmann, 1967, p. 538.

Syntypes.—Bingh. Oceanogr. Coll. 2300, 2 (110-113). Eastern tropical Pacific off Mexico, 16° 14' N, 99° 36' W. (Otter trawl: 1140 mwo), May 31, 1926. Parr referred to these two specimens as "type" (110 mm.) and "cotype" (113 mm.) in 1931 (p. 36) but did not distinguish between them in his original description.

Comparative diagnosis.—A species of Scopelarchoides with 6-7 dorsal rays, 20-23 anal rays, 20-23 pectoral rays, and 46-50 lateral line scales; pelvic fins distinctly longer than pectorals, both lacking pigment; dermal pigment heavily concentrated in a broad stripe ventral to lateral line; gill filaments extremely elongate, overlapping pectoral base. The combination of these characters distinguishes *S. nicholsi* from all other known scopelarchids.

Description.—Based on 82 (8.1-39.5) larvae and metamorphosing specimens and 157 (40.0-115.5) adolescents and adults. With the exception of meristic characters, the description based upon adults is given first, followed by an account of development.

MERISTIC CHARACTERS: Values listed in parentheses are those of the syntypes (taken from Parr, 1929, p. 16). Dorsal 6-7 (6); anal 20-23 (21-23); pectoral 20-23 (20-22); lateral line scales 46-50 (ca. 50); vertebrae 45-48 (48).

PROPORTIONAL DIMENSIONS: Expressed as thousandths of the S.L. and given as the mean, range (values in brackets), and values for the syntypes (values in parentheses). Based on 10 (46.0-111.3) specimens: Body, depth at dorsal origin, 174 [154-198] (170-180). Caudal peduncle: least depth, 78 [67-85] (70-80); length, 132 [122-136]. Adipose fin: distance to midcaudal rays, 186 [178-196] (180-190); length of base, 40



FIG. 43. Scopelarchoides nicholsi Parr. A. Young adult, SIO 73-252,1 (62.5) B-D. Lateral line scales, SIO65-243, 104.1. B.Lateral line scale above anal origin. C. Lateral line scale above pectoral insertion. D. Penultimate lateral line scale.

[35-49]; length of fin, 68 [59-74]. Anal fin: length of base, 273 [256-297] (260); length of longest ray, 133 [114-163]. Dorsal fin: length of base, 40 [37-46]; length of longest ray, 102 [85-120]; dorsal origin to anal origin (distance between verticals), 218 [200-242]; end of dorsal base to base of midcaudal rays, 595 [576-626]. Pectoral fin, length of longest ray, 173 [150-190] (160-170). Pelvic fin, length of longest ray, 208 [185-227] (230-240). Pelvic insertion to anal origin, 172 [141-202]. Pectoral insertion to pelvic insertion, 152 [144-166]. Anus to anal origin, 50 [42-60]. Distance from snout to: anus, 552 [533-589]; dorsal origin, 387 [383-396] (370-390); anal origin, 592 [580-618] (600-630); pectoral insertion, 283 [272-302]; pelvic insertion, 429 [404-444] (410-420); orbit. 66 [59-73] (60-70). Head length, 261 [246-273] (250). Postorbital head length. 121 [114-130]. Orbit: horizontal diameter, 74 [70-79] (59-73); vertical diameter, 70 [66-75]. Interorbital width, 28 [17-43]. Upper jaw length, 160 [149-174]. Lower jaw length, 181 [174-196] (170-180). Longest dentary tooth, 26 [19-33].

BODY: Body moderately elongate, deep, strongly compressed. Body depth 5.79 [5.05-6.50] in S.L. Peduncle depth 3.38 [3.10-4.00] in H.L. Peduncle length 1.98 [1.81-2.17] in H.L.

SKIN AND SCALES: Body and postorbital region of head completely covered with cycloid scales. Three-four vertical rows of scales on cheek, 4-5 rows on opercle-subopercle. Largest body scales present behind pectoral insertion, considerably larger than adjacent body scales, and slightly larger than lateral line scales above pectoral insertion or anal origin. Body scales moderately large, five rows from lateral line to dorsal origin, six rows from lateral line to anal origin. About 26 rows from occiput to dorsal origin and about 32 rows from dorsal origin to adipose fin origin. Lateral line scales moderately large, numbering 46-50 in 48 specimens counted. Lateral line scale above anal origin, based on 20 (56.6-115.5) specimens: height/length, 1.10 [1.00-1.23]; tympanum height/length, .747 [.640-.835]; pore height/length, .263 [.219-.300]; height of scale slightly less than length; tympanum large, completely covering pore, alate laterally and rounded or slightly indented at anterior margin. Lateral line scale above pectoral insertion, based on 10 (54.1-110.5) specimens: height/length, 1.08 [.95-1.27]; tympanum height/length, .589 [.539-.634]; pore height/length, .237 [.200-.333]. Penultimate lateral line scale, based on 10 [74.3-110.5] specimens: height/length, 1.49 [1.23-1.67]; tympanum height/length, 1.01 [.852-1.31]; pore height/ length, .288 [.238-.342]; length considerably less than height and usually less than tympanum height; tympanum very broad, alate, completely covering pore. Ultimate lateral line scale, based on 4 [75.7, 87.3, 103.0,

104.3] specimens and listed in that order: height/length, 1.06, 1.08, 1.07, 1.06; ultimate lateral line scale imperforate, reaching nearly to bases of midcaudal rays, circuli present on anterior three-fourths of length.

HEAD: Dorsal profile rounded and descending steeply to rounded snout. Eye diameter greater than snout length. Head depth slightly less than body depth, head width subequal to body width. Eyes directly slightly dorsoanteriad. Pearl organ a dorsally and ventrally flattened ellipse with major axis normal to visual axis. Head length 3.83 [3.67-4.05] in S.L. Snout length 3.98 [3.64-4.50] in H.L. Horizontal eye diameter 3.54 [3.20-3.76] in H.L. Postorbital head length 2.16 [2.04-2.32] in H.L. Interorbital width 10.22 [6.20-15.30] in H.L.

Head densely pigmented on all external surfaces with especially dense pigment on occiput, dorsal margins of eye, as a dark streak anterior to eye, snout, lining of dentigerous surfaces of jaws, and ventrally on mandible, but absent from branchial and oral cavities. Light pigment on branchiostegal membranes between branchiostegal rays 1-4 (counted from anterior to posterior).

Opercle much larger than subopercle, rounded and nonserrate posteriorly, reaching nearly to a vertical from pectoral insertion. Pectoral insertion opposite opercle-subopercle border but no notch in gill cover occurs at this point.

Pseudobranchiae well-developed. Counts: (47.6) 9; (53.5) 10; (70.6) 10; (87.3) 11; (103.2) 10. Gill filaments extremely elongate and extending beyond margins of gill covers, overlapping pectoral insertion posteriorly. Gill membranes united under anterior margin of eye.

MOUTH: Upper jaw length 1.64 [1.54-1.76] in H.L. Lower jaw length 1.45 [1.38-1.53]. Upper jaw extends to vertical through posterior margin of eye.

Tooth counts based on 5 [47.6, 63.5, 70.6, 87.3, 103.2] specimens and listed in that order. Premaxillary tooth counts: 26, 35, 49, 58, 69. Dentary tooth counts: lateral 15, 17, 19, 26, 33; medial 7, 6, 10, 9, 9. Longest dentary tooth 10.47 [8.34-13.80] per cent H.L. Palatine tooth counts: 12, 11, 13, 15, 16. Vomerine teeth small, one per side except in one specimen with one present on one side and two on the other side. Lingual teeth over shortened basihyal, and all three basibranchials but present only at anterior end of third basibranchial. Counts: 9, 9, 11, 16, 15.

FINS: Dorsal moderately long, longest dorsal ray 10.2 [8.5-12.0] per cent S.L. Dorsal base short, 4.0 [3.7-4.6] per cent S.L. Pelvics inserted beneath or behind a vertical from middorsal fin base, and inserted beneath or slightly behind last dorsal ray in largest adults. Appressed pelvic fins reach slightly beyond anal origin. Pelvic fin rays consider-

ably stouter and longer than pectoral rays. Length of longest pelvic ray 20.8 [18.5-22.7] per cent S.L.; length of longest pectoral ray 17.3 [15.0-19.0] per cent S.L. Anal base moderate, 27.3 [25.6-29.7] per cent S.L. Anal origin well behind midlength, preanal distance 59.2 [58.0-61.8] per cent S.L.

COLOR: Body completely covered with pigment, with pigment especially dense around and outlining scale pockets. Peritoneum remains prominently visible in all but largest available adults due to apparent tardiness of investiture of abdominal body wall with musculature. Dorsal fin heavily pigmented. Pigment limited to bases of pectoral, pelvic, and anal fins with no pigment on rays or membranes. Peduncle outlined with intense black pigment at base of dorsal and ventral procurrent rays and caudal ray bases. Both lobes of caudal fin covered with dense pigment to tip of fin. Dermal pigmentation concentrated in a broad stripe ventral to lateral line with noticeably less dermal pigmentation dorsal to lateral line.

Development.—The description of development in Scopelarchoides nicholsi is based on 81 (8.1-39.5) larval and metamorphic specimens and 64 (40.0-63.5) adolescent and young adult specimens. Figure 44 illustrates in sequence the development of this species.

RECOGNITION: Larvae of *S. nicholsi* can be distinguished through the following combination of characters: dorsal 6-7; anal 20-23; pectoral 20-23; one peritoneal section only in larvae to 26-30 mm. in size; paired posterior sections appear in advance of vertical from pelvic insertion and coincident with appearance of paired sections is appearance of dermal pigmentation on peduncle and pigmentation at posterodorsal angle of mandible; unique combination of up to three accessory pigment spots, one on each side of caudal peduncle at terminus of lateral line just anterior to bases of midcaudal rays, one midventral spot just behind last anal ray, one midventral spot behind pelvic fin base and just ventral to ventral contour of intestine; no dorsal accessory spot.

BODY: Body moderately short, deep, with moderately deep peduncle. Head relatively large, one-fourth or more of standard length in larvae up to 30 mm.

FINS: In smallest available specimen [S1063-1092, 1 (8.1)] there are no ossified fin rays and the notochord is undergoing flexure. Caudal fin rays are ossified in 10-12 mm. specimens and all fin rays are ossified by 26-28 mm. specimens. Apparent order of ossification of fin rays: caudal, anterior anal rays, dorsal, dorsal pectoral rays, posterior anal rays, pelvic, ventral pectoral rays. Pelvic fins appear as buds beneath or



F1G. 44. Development of *Scopelarchoides nicholsi*. A. SIO68-617, 9.1. B. SIO68-617, 24.5. C. SIO65-253, 30.0. D. SIO65-243, 47.5.

behind vertical through middle of dorsal base, above gut. Pelvic insertion in larger larvae beneath or behind vertical through middle of dorsal base. Ventral adipose fin two-thirds pelvic-anal distance in smaller larvae and lost during metamorphosis. Dorsal adipose remains elongate, to over anterior anal rays, throughout metamorphosis but assumes adult dimensions in 40-50 mm. specimens.

PERITONEAL SECTIONS: Three peritoneal sections. Single transverse dorsomedial section over gut and between pectoral fin bases appears in

smallest larvae, and remains as transverse sheet until onset of metamorphosis. Two paired peritoneal sections appear as pigment spots near ventrolateral body wall in advance of vertical through pelvic insertion and signal onset of metamorphosis in 26-28 mm. larvae. During metamorphosis both anterior and posterior sections expand posteriorly, eventually coalescing and forming complete tube around gut at completion of metamorphosis.

ACCESSORY PIGMENT SPOTS: A maximum of three accessory pigment spots. Two midlateral pigment spots (PDA) on either side of caudal peduncle at terminus of lateral line. An unpaired midventral spot just behind last anal ray (PA). A midventral pigment spot behind pelvic base and just ventral to ventral contour of intestine (IA). All three pigment spots well-developed in smallest available larvae. PDA retained and evident in largest adults. PA overgrown by skin and muscle tissue and appears to sink during metamorphosis, but is retained in largest adults. I have not found an IA in specimens larger than 25.2 mm. and the IA is presumably lost before or during metamorphosis.

DERMAL PIGMENTATION: Appearance of dermal pigmentation coincident with appearance of paired posterior peritoneal sections in 26-28 mm. larvae. Dermal pigmentation essentially covers body in larvae 36 mm. and larger. First dermal pigmentation on body appears on caudal peduncle in association with and anterior to PDA. This pigmentation rapidly expands to cover caudal peduncle from middorsal to midventral, and spreads forward on both epaxial and hypaxial surfaces as evenly scattered large melanophores. Hypaxial pigmentation spreading forward more rapidly than epaxial pigmentation, but not concentrated into characteristic hypaxial stripe in specimens smaller than 40 mm. Pigmentation on head appears first as patch of melanophores at posterodorsal angle of mandible. Additional pigment appears at mandibular symphysis, occipital region, around orbit, on interorbital region, and on snout, and the head pigmentation is similar to that described for adults in specimens 36 mm. and larger.

GUT: Post-pelvic gut length in smallest larvae about one-third pelvicanal distance, increasing during growth and reaching one-half to twothirds pelvic-anal distance in metamorphic specimens, reaching essentially adult dimensions in specimens 45 mm. and larger. Caecum expansion begins at onset of metamorphosis (26-28 mm.), increasing in length posteriorly throughout metamorphosis, and reaching nearly to anus in specimens 45 mm. and larger.

METAMORPHOSIS: Changes in metamorphic larvae 26-40 mm. in size have been described above, and lead essentially to adult form and pigmentation except for three changes occurring in 40-45 mm. larvae



FIG. 45. Distribution of *Scopelarchoides nicholsi*. Large solid circles = larvae. Large open circles = adults. Small solid dots = distribution of *Rosenblattichthys volucris*. Stippling, encloses areas of subsurface waters of low oxygen concentration, with dissolved oxygen less than 0.15 ml/l below the thermocline (after Brandhorst, 1959). Southern boundary in southern hemisphere is not shown.

that are somewhat arbitrarily used as the breaking point between metamorphic specimens and adolescents. In the 40-45 mm. size range the anterior and posterior peritoneal sections coalesce at a line of fusion slightly in advance of a vertical through the pelvic insertion, the peritoneal pigment expands laterally and forms a complete tube around the gut, and a definite concentration of hypaxial dermal pigmentation produces the characteristic hypaxial stripe of the adults. Investiture of the abdominal body wall by musculature is extremely delayed in *Scopelarchoides nicholsi*, and is not complete, although layers of muscle tissue can be seen, in the largest adults.

Distribution .-- Scopelarchoides nicholsi is restricted to the eastern

Pacific Ocean (fig. 45) in those areas of the Pacific Equatorial Water Mass exhibiting the greatest development of a subsurface layer of poorly oxygenated water (Brandhorst, 1959). The distribution of this species is disjunct, with a northern area extending from the vicinity of Cedros Island, Baja California (ca. 27° N) to 5-9° N, and west to 136° W, and a southern area off Peru from 6° S to 12-13° S and west to 87° W. S. *nicholsi* has not been taken in the intervening equatorial area. This area is occupied by *Rosenblattichthys volucris* (fig. 36) and *Scopelarchus* guentheri (fig. 55), which are, however, not restricted to it. Numerous captures of specimens of these latter two species at depths appropriate to the capture of S. *nicholsi*, especially captures of larvae (larvae of all three species dwell in the upper 100-150 m.) indicates that the disjunction in range of S. *nicholsi* is real, and not an artifact of sampling.

Larvae and adults of *S. nicholsi* have been taken in both areas of its distribution throughout the year. A large number of adult *S. nicholsi* (larger than 60 mm. S.L.) have been taken in tows at night to depths between 115-140 in., and larvae and adolescents have been taken frequently in the upper 100 m. at night. The shallowest successful daytime tow was to 346 m., but there have been very few successful daytime tows. Thus *S. nicholsi* occurs at relatively shallow depths, for a scopelarchid, at least at night. This might be related either to the shallow depth of the thermocline in this area (Wyrtki, 1964) or may be related to the poorly oxygenated subsurface layers. Other midwater fish species have been noted to occur at unusually shallow depths in the eastern tropical Pacific (e.g., Alverson, 1961).

Material examined.-A total of 241 (8.1-115.5) specimens from 100 collections. DANA: D1208 I. 2 (63,5-106.0); D1209 I, 1 (85.5); D1209 IV; I (32.8); D3549 VI, 2 (41.7-104.3). FMNH; FMNH 71602, 2 (55.0-56.0). LACM: LACM 8274, 1 (33.0); LACM 8284, 1 (102.1); LACM-E 10284, 2 (58.7-59.6). NMFS: HMS 31-35, 1 (36.5); HMS 31-47, 2 (14.5-17.0); HMS 31-54, 1 (37.0); HMS 31-62, 1 (44.9). SIO: SIO52-425, 2 (16.1-26.0); SIO54-88, 7 (57.0-76.8) S1055-213, 3 (20.0-56.3); S1055-229, 1 (40.3); S1055-231, 2 (67.4-91.2); S1059-201, 1 (89.0); S1060-553, 9 (9.5-22.0); S1063-899, 2 (26.4-41.1); S1063-905, 2 (34.8-42.6); \$1063-915, 3 (25,5-51,5); \$1063-917, 2 (17,5-38,2); \$1063-952, 1 (40,5); \$1063-959, I (38,1); S1063-962, 1 (71.0); S1063-965, 2 (32.0-49.0); S1063-966, 1 (40.0); S1063-968, 1 (27.0); \$1063-970, 1 (75.0); \$1063-973, 1 (22.1); \$1063-999, 12 (26.0-48.0); \$1063-1000, 3 (31.8-34.5); S1063-1001, 1 (27.0); S1063-1026, 1 (31.5); S1063-1029, 2 (38.0-60.0); S1063-1035, 2 (33.0-49.0); S1O63-1092, 4 (8.1-16.5); S1O64-15, 1 (84.0); S1O64-171, 1 (35.1); S1O65-220, 2 (36.3-55.0); SIO65-232, 1 (38.0); SIO65-236, 1 (38.2); SIO65-241, 5 (41.5-74.3); \$1065-243, 9 (16.5-104.1); \$1065-244, 2 (75.7-103.0); \$1065-251, 3 (57.5-68.0); \$1065-253. 1 (30.0); S1O65-577, 1 (39.2); S1O65-582, 1 (49.0); S1O65-603, 1 (58.0); S1O65-608, 1 (21.9); S1065-614, 8 (24.0-45.0); S1068-50, 14 (16.6-110.2); S1068-54, 1 (27.2); S1068-65, 1 (63.8); S1068-81, 1 (70.6); S1068-132, 4 (47.8-74.2); S1068-617, 6 (9.1-28.1); S1069-450, 1 (39.5); S1069-455, 1 (42.5); S1069-456, 1 (45.4); S1069-459, 1 (53.5); S1073-252, 1 (62.5); S1O, uncat., 1 (37.2). SOSC: AB 16-650H, 1 (25.0); AB 16-650R, 9 (32.8-65.5); AB 16-655D, 7 (41.7-105.2); AB 16-655F, 1 (62.5); AB 16-656A, 2 (88.2-89.6); AB 16-656L, 6 (31.9-80.5); AB 16-656-0, 1 (42.6); AB 16-656P, 3 (48.6-77.8); AB 16-656Q, 2 (76.1-83.2); AB 18B-755, 2 (52.1-63.6). USC-V: 13728, 1 (28.0); 13729, 1 (46.0); 13736, 1 (41.5); 13738, 1 (54.0); 13740, 2 (43.4-49.5); 13750, 1 (106.4); 13751, 3 (45.1-102.7); 13757, 1 (50.0); 13758, 2 (103.7-112.6); 13759, 1 (114.0); 13760, 2 (99.7-111.3); 13762, 2 (55.0-56.6); 13763, 11 (51.1-115.5); 13772, 1 (111.3); 13777, 4 (75.5-87.1); 13778, 2 (mutil.-106.5); 13779, 3 (70.0-113.4). USNM: USNM 148238, 1 (64.7); USNM 201154, 4 (46.0-56.7); USNM 201155, 4 (38.5-79.0); USNM 201156, 3 (41.3-58.2); USNM, uncat., H6204, 120.50, 1 (40.1).



FIG. 46. Scopelarchoides signifer. A. Holotype, S1068-534, 81.8. B-D. Lateral line scales. B. Lateral line scale above anal origin, ORSTOM 21/2/69, 83.0. C. Lateral line scale above pectoral insertion, DANA 3678 VII, 70.0. D. Penultimate lateral line scale, ORSTOM CYCLONE V-2, 104.6.

Scopelarchoides signifer Johnson 1974. Figure 46.

Scopelarchoides signifer Johnson 1974, pp. 454-455.

Holotype.—81.8 mm. S.L. Central Equatorial Pacific. S1O68-534. 00° 00-03.7' N, 165° 42.5-46.0' W. [IKMT: 2550 mwo (20 min.) 1800 mwo (20 min.)], August 11-12, 1968.

Comparative diagnosis.—A species of Scopelarchoides with 9-10 dorsal rays, 26-29 anal rays, 22-25 pectoral rays, and 49-52 lateral line scales; pectoral fins longer than pelvic fins; origin of pelvic fins under anterior one-third of dorsal base; heavy pigmentation on dorsal lobe of caudal fin but pigment absent or very weakly developed on ventral lobe of caudal fin. The combination of these characters distinguishes Scopel-archoides signifer from all other known scoparchids.

Description.—Based on 171 (4.8-29.8) larval and metamorphic specimens and 36 (32.2-104.6) adolescent and adult specimens. With the exception of meristic characters, the description based upon adults is given first followed by an account of development.

MERISTIC CHARACTERS: Values in parentheses are those of the holotype. Dorsal 9-10 (9); anal 26-29 (27); pectoral 22-25 (24); lateral line scales 49-52 (51); vertebrae 48-49 (49).

PROPORTIONAL DIMENSIONS: Based on 10 (36.6-99.0) specimens: Western Pacific, DANA 3678 VII, 2 (60.0-70.0); DANA 3685 X, 1 (62.6); DANA 3731 X, 1 (99.0); DANA 3800 II, 1 (73.1); SIO61-32, 1 (42.1); Central Equatorial Pacific, SIO68-534, 4 (36.6-81.8) including holotype. Expressed as thousandths of the standard length and given as the mean, range (in brackets), and values for the holotype (in parenthesis).

Body, depth at dorsal origin, 136 [112-159] (134). Caudal peduncle: least depth, 74 [67-81] (71); length, 121 [110-131] (123). Adipose fin: distance to midcaudal rays, 174 [166-186] (183); length of base, 39 [26-45] (43); length of fin, 55 [41-65] (56). Anal fin: length of base, 336 [326-348] (341); length of longest ray, 102 [82-116] (88). Dorsal fin: length of base, 60 [56-67] (61); length of longest ray, 117 [94-154] (98); dorsal origin to anal origin (distance between verticals), 202 [185-223] (203); end of dorsal base to base of midcaudal rays, 574 [565-583] (580). Pectoral fin, length of longest ray, 167 [128-200] (128). Pelvic fin, length of longest ray, 106 [76-128] (111). Pelvic insertion to anal origin, 155 [138-179] (153). Pectoral insertion to pelvic insertion, 177 [170-188] (174). Anus to anal origin, 61 [43-83] (48). Distance from snout to: anus, 507 [478-535] (507); dorsal origin, 374 [358-399] (373); anal origin, 555 [539-580] (559); pectoral insertion, 241 [222-259] (238); pelvic insertion, 408 [396-421] (396); orbit, 60 [55-65] (57). Head length, 225 [220-233] (226). Postorbital head length, 90 [80-108] (86). Orbit: horizontal diameter, 76 [57-88] (80); vertical diameter, 72 [55-82] (68). Interorbital width, 18 [14-24] (15). Upper jaw length, 144 [123-132] (160). Lower jaw length, 159 [137-176] (160). Longest dentary tooth, 20 [16-24] (20).

BODY: Body moderately elongate, relatively shallow but massive. Body depth 7.43 [6.30-8.93] (7.44) in S.L. Peduncle depth 3.05 [2.76-3.36] (3.19) in H.L. Peduncle length 1.86 [1.68-2.06] (1.83) in H.L.

SKIN AND SCALES: Body and head scales and scale pockets missing from all specimens examined, except for two specimens retaining large cycloid scales behind pectoral fin base. Scales behind pectoral base large, deeper than anal lateral line scales, truncate anteriorly, with large central focus, and many more circuli in anterior than in posterior field. Lateral line scales numbering 49-52 in 20 specimens counted. Lateral line scales large in both vertical and horizontal dimensions. Lateral line

scale above anal origin based on 16 (42.1-104.6) specimens [Western Pacific, 5 (60.0-83.0); Central Equatorial Pacific, 11 (42.1-104.6)]; height/length, 1.46 [1.32-1.62] (1.29); tympanum height/length, 1.02 [0.790-1.21] (1.00); pore height/length, .381 [.337-.444] (.359); tympanum very large, alate, smoothly but distinctly indented at anterior margin, usually not completely covering large central pore. Lateral line scale above pectoral insertion, based on 5 (60.0-83.0) specimens [West-(60.0-73.1); Central Equatorial Pacific, 2 (73.5ern Pacific. 3 83.0)]: height/length, 1.28 [1.09-1.41]; tympanum height/length, .841 [.650-.929]; pore height/length, .354 [.304-.436]; tympanum indented anteriorly, alate but dorsal wing of tympanum distinctively more than twice as deep as ventral wing, incompletely covering large central pore. Penultimate lateral line scale, based on two [Central Equatorial Pacific, 73.5-104.6] specimens and listed in that order: height/length, 1.21, 1.64; tympanum height/length, .693-1.13; pore height/length, .366-.396. Ultimate lateral line scale missing from all specimens examined, probably due to damage during capture, but from shape of ultimate scale pocket probably extends nearly to base of midcaudal rays.

HEAD: Dorsal profile moderate, descending gradually from occiput to rounded snout. Eye diameter noticeably greater than snout length. Head depth and width subequal to body depth and width. Head length 4.44 [4.29-4.54] (4.42) in S.L. Snout length 3.78 [3.48-4.05] (3.94) in H.L. Horizontal eye diameter 2.99 [2.59-3.86] (2.84) in H.L. Postorbital head length 2.51 [2.10-2.92] (2.64) in H.L. Interorbital width 13.15 [9.00-15.70] (15.40) in H.L.

Occiput, dorsoposterior corner of orbit, interorbital area, snout, anterior and lateral surface of premaxillary; anterior and lateral surface of mandible (but not anteroventral surface of mandible) densely pigmented. A layer of guanine below first infraorbital. A dense streak of pigment bordering anterior margin of eye.

Opercle plowshare-shaped, smaller than subopercle, distinctly serrate at dorsoposterior margin. Pectoral insertion opposite a deep notch at opercle-subopercle border.

Pseudobranchiae well-developed. Counts: (81.0) 16: (99.0) 18. Gill filaments not extending to edge of gill covers. Gill membranes united under anterior one-third of eye.

MOUTH: Upper jaw length 1.57 [1.46-1.83] (1.61) in H.L. Lower jaw length 1.42 [1.29-1.55] (1.41) in H.L. Upper jaw terminates under posterior one-third of eye.

Tooth counts based on 4 (33.2, 52.9, 81.8, 99.0) specimens and listed in that order. Premaxillary tooth counts 28, 42, 62, 82. Dentary tooth

counts, lateral, 24, 31, 46, 63; medial, 8, 9, 10, 14. Longest dentary tooth 11.32 [9.70-14.40] (10.50) in H.L. Palatine tooth counts 13, 11, 18, 22. Lingual teeth essentially limited to basihyal, at most one or two very small teeth situated over first basibranchial. Counts: 8, 10, 10, 14.

FINS: Dorsal relative high, length of longest dorsal ray 11.7 [9.4-15.4] per cent S.L.; length of dorsal base 6.0 [5.6-6.7] per cent S.L. Pelvics inserted under anterior one-third of dorsal base. Appressed pelvics reach past anus nearly to anal origin. Pectoral rays noticeably longer than pelvic rays. Length of longest pelvic ray 10.6 [7.6-12.8] per cent S.L.; length of longest pectoral ray 16.7 [12.8-20.0] per cent S.L. Appressed pectoral fins reaching behind pelvic insertion, nearly to anus. Anal base elongate, 33.6 [32.6-34.8] per cent S.L. Anal origin well behind midlength, preanal distance 55.5 [.33.9-58.0] per cent S.L.

COLOR: Dermal pigment apparently lacking from body. Pigment weakly developed at base and along one-third length of first four to five dorsal rays. Pigment well-developed on membrane overlying dorsal procurrent rays, scaly flaps of skin overlying caudal fin ray bases, and along entire length of dorsal lobe of caudal fin. Pigment absent or very weakly developed (in largest specimens) on ventral procurrent rays and ventral lobe of caudal fin.

Development.—The description of development in Scopelarchoides signifer is based on 168 (4.8-29.8) larval specimens and 20 (32.2-60.0) adolescent and young adult specimens. Figure 47 illustrates in sequence the development of this species.

RECOGNITION: Larvae of S. signifer can be distinguished by the following combination of characters: dorsal 9-10; anal 26-29; pectoral 22-25; one peritoneal section only, appearing dorsal to gut in anterior of abdominal cavity and expanding posteriorly and laterally with growth; unique combination of two accessory pigment spots, one middorsal on caudal peduncle (DA) and one directly below in midventral caudal peduncle immediately behind last anal ray (PA); no PDA or IA; no pigment on pectoral fin.

BODY: Body short, deep, with moderately deep peduncle. Head relatively large, one-fourth or more of S.L. in larvae up to 30 mm.

FINS: No ossified fin rays in smallest (4.8-7.0) available larvae. Notochord flexure occurs in larvae 5-6 mm. Caudal fin rays ossified in larvae 8 mm. and larger, and all fin rays are ossified in larvae 25 mm. and larger. Apparent order of fin ray ossification: caudal, dorsal, anal, dorsal pectoral, pelvic, ventral pectoral. Pelvic fins appear as buds beneath or slightly behind last dorsal ray in midlateral abdominal cavity wall, about one-half of abdominal cavity depth (from ventral contour to



FIG. 47. Development of *Scopelarchoides signifer*. A. DANA 4820,9.0. B. DANA 3950 I, 11.4. C. S1070-121, 22.6.

muscle mass delimiting abdominal cavity dorsally) from ventral contour of body, well above intestine. Pelvic fin bases remain entirely above (dorsal to) gut in specimens smaller than 25-26 mm. Pelvic insertion in larger larvae, 25-30 mm., beneath middorsal base, pelvic insertion in adults under anterior one-third of dorsal base. Ventral adipose base remains about two-thirds of pelvic-anal fin distance in larvae up to 25-30 mm., and ventral adipose lost in specimens larger than 30 mm. Dorsal adipose remains elongate, to over anterior one-third of anal base, throughout metamorphosis but assumes adult proportions in specimens 30-35 mm. and larger.

PERITONEAL SECTIONS: Only one peritoneal section. Peritoneal section present in smallest known larva, 4.8 mm., at anterior of abdominal cavity forming a canopy over anterior part of gut, with two large

lateral wings connected dorsally. Peritoneal section retaining this configuration throughout metamorphosis. In specimens 30 mm. and larger peritoneal pigment section begins rearward and laterad extension, expanding posteriad more rapidly than laterad, reaching full rearward extension in specimens 40 mm. and larger but not connecting ventrally until specimens 50-60 mm. in size. Complete tube around gut present in specimens 60 mm. and larger.

ACCESSORY PIGMENT SPOTS: Two accessory pigment spots, DA and PA. PA behind last anal ray on midventral line of caudal peduncle. DA directly or almost directly above PA on middorsal line of caudal peduncle. Both absent in two larvae 4.8-5.0 mm. PA present in one specimen, 5.9 mm., but apparently no DA. Both PA and DA present in all specimens (including adults) larger than 7 mm. PA and DA overgrown by skin and muscle in larger specimens, but are still present in largest known adult, 104.6 mm.

DERMAL PIGMENTATION: Dermal pigment on body apparently lacking in this species. Pigment on upper lobe of caudal fin first appears in specimens 45 mm. and larger and presenting typical flag-like appearance in specimens 50 mm. and larger.

GUT: Post-pelvic gut length about one-third pelvic-anal distance in larvae smaller than 25 mm. Anus immediately in advance of anal origin in specimens 30 mm. and larger. Gut behind pelvic base outside of main portion of abdominal cavity in larvae, hanging in a thin flap of tissue situated beneath main portion of abdominal cavity, with anus reaching nearly to distal anterior edge of ventral adipose fin. Flap supporting anus reabsorbed with growth and post-pelvic gut within abdominal cavity and reaching nearly to anal origin in specimens 25-30 mm. and larger. Rearward expansion of caecum first evident in specimens 30-35 mm., expanding slowly rearward with growth, reaching about one-half of pectoral-pelvic distance in specimens 30-40 mm., reaching nearly to pelvic insertion in 40-50 mm. specimens, and reaching slightly past pelvic base in specimens 50 mm. and larger, apparently never reaching near anus.

METAMORPHOSIS: Metamorphosis gradual in this species with adult characters acquired one by one over the increment of growth between 20 and 60 mm. Although metamorphosis is not complete until individuals reach 50-60 mm. in size, when the peritoneal section joins ventrally to form a complete tube around the gut and the caecum exhibits its maximum rearward expansion, adult appearance is achieved by complete investiture of abdominal cavity wall with musculature with concomitant placement of pelvic fin bases at ventrolateral contour of body. Thus, somewhat arbitrarily, specimens smaller than 30 mm. in size are





referred to as larvae while those greater than 30 mm. are termed adolescents and adults.

Distribution.—Scopelarchoides signifer is apparently limited to the Pacific and Indian Oceans (fig. 48). It has been taken throughout the Indian Ocean from ca. 25° S off southern Africa to 02° N off Sumatra. It occurs in the South China Sea and in the semi-isolated seas of the Indo-Malayan Archipelago. In the Pacific S. signifer is known from numerous specimens in a narrow band along the equator within 5° of latitude north and south of the equator, and extending east to ca. 138° W. The only other Pacific records are from the Climax stations near 24.5° S, 155° W.

Larvae of *S. signifer* have been taken throughout the year and throughout the range of the species. Larvae have been captured in numerous hauls to depths less than 50 m., and apparently occur predominantly in the upper 100 m. Most adults have been taken in hauls to between 300 and 500 m. in depth, the shallowest night-time record a haul from 0-300 m., the shallowest daytime record a haul from 0-280 m. I am aware of only five daytime hauls that captured this species.

Material examined.—A total of 208 (4.8-104.6) specimens from 104 collections. Indian Ocean. DANA: 3805 b, 2 (12.0-12.1); 3806, 4 (10.0-16.1); 3817 111, 2 (8.6-10.5); 3819 1, 1 (10.1); 3821 11, 1 (13.6); 3821 111, 10 (10.5-23.0); 3821 1V, 3 (15.0-16.5); 3844 V11, 1 (10.5); 3844 V111, 2 (9.5-11.0); 3851 11, 2 (5.2-9.6); 3853 1, 1 (10.6); 3858, 1 (9.6); 3889 1, 1 (16.0); 3915 11, 2 (ca. 33-42.4); 3919 111, 1 (14.0); 3919 V, 11 (9.1-12.1); 3920 V, 1 (15.1); 3920 X, 4 (13.6-15.2); 3926 111, 1 (16.0); 3930 1V, 1 (14.5); 3931 1V, 1 (14.1); 3934 V, X, XV, XXX, 1 (10.2); 3944 11, 1 (7.0); 3944 111, 3 (10.2-14.5); 3948 111, 4 (10.0-11.6); 3949 1V, 14 (9.0-21.8); 3949 1V, 1 (8.5); 3950 1, 11 (4.8-11.4); 3951 111, 8 (5.1-20.5); 3952 111, 2 (9.4-20.5); 3952 111, 3 (8.9-11.8); 3952 1V, 4 (12.8-14.8); 3953 1, 2 (18.5-21.0); 3953 11, 7 (7.5-22.8); 3953 111, 9 (10.0-23.4); 3953 1V, 1 (12.0); 3954 111, 1 (10.9); 3955 1, 2 (24.0-25.9); 3964 111, 3 (25.2-29.2); 3964 111, 3 (7.1-16.9); SOSC: AB 6-339A, 1 (15.5); TV 4-168, 1 (21.1); USNM: uncat. HOE material, AB VI-336B, 1 (14.1); AB VI-337A, 1 (54.6).

Western Pacific. DANA: 3678 V11, 2 (60.0-70.0); 3685 X, 1 (62.0); 3731 X, 1 (99.0); 3800 11, 1 (73.1); 3800 1V, 2 (12.0-15.0); 3804 1V, 1 (12.0); 4768, 7 (12.1-18.6); 4820, 5 (8.0-18.0); SIO: 61-32, 1 (42.1); 61-540, 2 (19.1-21.5); 70-344, 1 (ca. 19).

Central equatorial Pacific. NMFS: HMS 31-173, 1 (62.5); HMS 31-176, 1 (mutilated); **ORSTOM:** 24/9/68, 1 (66.0); 4/10/68, 1 (78.1); 21/2/69, 1 (83.0); Caride 1-100A, 1 (77.5); Cyclone 11-12, 2 (52.9-73.5); Cyclone 11-14, 3 (45.6-48.5); Cyclone 11-15, 4 (32.2-48.9); Cyclone 11-18, 1 (ca. 40); Cyclone 1V-5, 1 (72.5); Cyclone V-2, 1 (104.6); **S10:** 60-236, 2 (39.5-49.1); 62-573, 2 (13.5-27.0); 68-534, 5 (33.0-70.0); 68-535, 4 (25.1-37.9); **SOSC**; TV 8-323, 1 (11.8).

Central South Pacific. S10: 70-118, 2 (28.5-29.8); 70-121, 2 (22.6-37.1); 70-122, 5 (11.0-26.6); 72-311, 1 (16.8).

Scopelarchus Alcock 1896

Scopelarchus Alcock, 1896, p. 306.

Dissomma Brauer, 1902, p. 278. Phanops Rofen, 1963, p. 4.

Type-species.—Scopelarchus guentheri Alcock, 1896, pp. 306-308.

Diagnosis.—Scopelarchids with parietals absent, antorbital absent, ethmoid process on first infraorbital present, basihyal short, lingual teeth present over first two basibranchials, suspensory pharyngobranchial absent, support of first epibranchial at point of articulation between second pharyngobranchial and second epibranchial, coracoid widely expanded, coracocleithral fenestra small, 40-51 vertebrae, 40-52 lateral line scales; dermal pigment present concentrated as two subequal stripes dorsal and ventral to lateral line extending forward from caudal peduncle; pelvic insertion beneath or behind middle of dorsal base to distinctly behind last dorsal ray; pectoral length exceeds pelvic length; larvae with three peritoneal sections, the posterior paired sections appearing well behind pelvic fin base, larvae lacking accessory pigment spots or areas, pelvic fin bud appearing ventrolaterally in abdominal cavity wall beneath or behind dorsal fin base.

Description.—Frontals greatly expanded, occupying one-half or more of postorbital dorsal skull roof; supraoccipital with low ridge of bone on posterior one-third of bone with a blunt knoblike protuberance at anterior end of ridge; opisthotic with anteroventrally directed prong; supramaxilla present only in *S. guentheri;* hyomandibular with only three rodlike arms; two extrascapulars.

Dorsal 7-9, anal 18-29, pectoral 18-22, lateral line scales 40-52, vertebrae 40-51.

Body relatively short, deep, massive, moderately compressed. Largest body scales behind pectoral insertion. Occiput, posterodorsal corner of orbit, snout, interorbital area, anterior and lateral premaxilla; anterior, lateral and ventroanterior mandible covered with dense pigment. No dark streak of pigment anterior to margin of eye. Scale pockets outlined with pigment dorsal but not ventral to lateral line. Pigment present on pectoral fin except in *S. guentheri*.

Larvae short to moderately elongate, with three peritoneal sections, appearing in near synchrony, the posterior paired sections appearing well behind the pelvic fin base; no accessory pigment spots or areas; dermal pigment present as stripes above and below the lateral line.

Comment.—Although a key to adult specimens of the genus *Scopelarchus* is provided, I have not constructed a key to the larvae of the species of *Scopelarchus*. This is because the larvae of this genus are so similar that it is very difficult to distinguish them. A key, based on any

other characters than fin-ray number would have to take into account. changes during increments of ontogeny, and thereby become unwieldy. The larval recognition sections of the species descriptions of *Scopelarchus* species should make possible the identification of *Scopelarchus* larvae above a certain minimum size.

KEY TO THE SPECIES OF Scopelarchus (specimens 30 mm. S.L. and larger)

Pigment on pectoral fin a limited patch of melanophores situated between second and sixth or seventh pectoral rays (counting from dorsalmost ray) on medial onethird of fin length, present neither at base nor on distal third of fin; appressed pectoral fin reaches level of pelvic insertion but not anus; caudal peduncle depth 7.9-9.2 per cent S.L.S. stephensi Johnson 1974 Central North Pacific.

Scopelarchus analis (Brauer 1902). Figure 49.

Dissomma anale Brauer, 1902, p. 278; 1906, pp. 138-139; 1908, p. 216. Zugmayer, 1911b, pp. 141-142. Weber, 1913, p. 84. Weber and De Beaufort, 1913, pp. 181-182. Barnard, 1925, pp. 247-248.

Evermannella balbo (nec. Risso, 1820.) Roule and Angel, 1930, p. 59.

Evermannella analis Roule and Angel, 1933, p. 32.

Odontostomus perarmatus Roule, 1916, p. 25; 1919, p. 32. Schmidt, 1918, p. 34.

- *Scopelarchus anale* Parr, 1928, pp. 159-162; 1929, pp. 12-14; 1931, p. 37. Gregory, 1933, p. 210. Beebe, 1937, p. 205. Norman, 1937, p. 86. Maul, 1946, pp. 17-20. Rey, 1947, pp. 383-386. Mead and Böhlke, 1953, p. 244. Koefoed, 1955, pp. 5-7. Grey, 1955, p. 284 (in part). McAllister, 1968, p. 95.
- *Scopelarchus analis* Fowler, 1936, pp. 353-354. Nybelin, 1948, pp. 40-44. King and Iversen, 1962, p. 320. Rofen, 1963, pp. 1-3; 1966e, p. 574 *et seq.* Smith, 1965, p. 114. Kotthaus, 1967, pp. 83-84.

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FIG. 49. Scopelarchus analis (Brauer). A. Adult, Bingham Oceanographic Collections 2131, 112.5. (Holotype of *S. candelops* Rofen, after Rofen 1966e, p. 577). B. Lateral line scale above anal origin, DANA 3624 1, 56.6. C. Lateral line scale above pectoral insertion, UH 70 9 24, 88.5. D-F. Scales from UH 70/7/24, 94.5. D. Penultimate lateral line scale. E. Ultimate lateral line scale. F. Body scale behind pectoral insertion.

- *Scopelarchus beebei* Rofen, 1963, pp. 1-3; 1966e, p. 574 *et seq.* Zahuranec et al., 1970, p. B-6.
- *Scopelarchus candelops* Rofen, 1963, pp. 1-3; 1966e, p. 574 *et seq.* Zahuranec et al., 1970, p. B-6.
- Scopelarchus guentheri Marshall, 1955, pp. 312-315 (in part). Craddock and Mead, 1970, p. 3.26 (in part).
- Scopelarchus perarmatus Rofen, 1963, pp. 1-3; 1966e, p. 574 et seq.
- *Scopelarchus sagax* Rofen, 1963, pp. 1-3, 1966e, p. 574 *et seq.* Zahuranec et al., 1970, pp. B-2, B-9.

Lectotype.—29.7 mm. S.L. Valdivia Station 50, Equatorial Atlantic, 00° 26.0' N, 6° 32' W. Deposited in Museum für Naturkunde, East Berlin.

Discussion.—The taxonomic history of Scopelarchus analis is the second longest and most complicated of any scopelarchid species. This species has at various times been included in three nominal families (Evermannellidae, Odontostomidae, Scopelarchidae) and four nominal genera. Five different specific names have been proposed based on specimens of this species. A majority of authors who were aware of S. guentheri Alcock believed S. guentheri and S. analis to be conspecific.

Most of the problems concerning the identity of this species stem from Brauer's ignorance of S. guentheri Alcock, and his consequent failure to provide diagnostic characters. Alcock's description of S. guentheri is also inadequate, but provides sufficient information that positive identification of S. guentheri was possible after enough specimens of both species had been examined and the range of variability of important characters determined. On the other hand, the type series of Dissomma anale Brauer contains at least two and perhaps three (or more) species. Thus it was necessary to re-examine Brauer's type material. Dr. Kurt Deckert of the Museum für Naturkunde, Humboldt Universitat, East Berlin, had the kindness to locate and re-examine the syntypes of D. anale from Valdivia stations 32, 50, 55, 66, and 182. He reports that the material is in very bad condition but was able to gather the following information from the largest specimen (taken at station 50): dorsal 8, anal 25, pectoral 22/22, pigment present on pectoral fin. As the shape of the lateral line scale above the anal origin differs between the two species, 1 provided Dr. Deckert with drawings and measurements of the lateral line scale above the anal origin for both S. guentheri and the species I had identified as S. analis. Dr. Deckert reports that in the syntype from station 50, the lateral line scale above the anal origin agrees well with my drawings for the form I called S. analis. The information supplied by Dr. Deckert taken in concert with Brauer's (1906, plate X, fig. 2) figure of this specimen establishes the identity of S. analis and clearly excludes the possibility that the specimen from station 50 could be referred to S. guentheri, S. michaelsarsi, S. stephensi, or any other scopelarchid species. It is fortunate that Brauer (1906, pp. 138-139) based not only his figure but his measurements on this same specimen. Therefore, the specimen from station 50 is selected as the lectotype of S.analis. My justification for synonomizing Scopelarchus beebei Rofen, S. candelops Rofen, S. perarmatus (Roule), and S. sagax Rofen with S. analis (Brauer) is given later in this paper.

Comparative diagnosis.—A species of *Scopelarchus* with 7-9 dorsal rays (197/226 or 87 per cent have dorsal = 8), 21-26 anal rays (228/237 or 96.1 per cent have anal = 22-25), 18-22 pectoral rays (226/237 or 95.4 per cent have pectoral = 19-21), 45-50 lateral line scales (143/148 or 96.5 per cent have lateral line scales = 46-49). *Scopelarchus analis* differs from *S. guentheri* in having pigment present on the pectoral fins cf. absent: 21-26 anal rays (usually 22-25) cf. 24-29 anal rays (usually 25-28); 18-22 pectoral rays (usually 19-21) cf. 18-19 in all populations of *S. guentheri* except those from the Subtropical Convergence and Eastern North Pacific off California and Baja California. Lateral line scale above anal origin moderately shallow with shallow tympanum and pore

[height/length, 1.33 (1.12-1.64); tympanum height/length .543 (412-.685); pore height/length, .233 (.176-.290)], cf. lateral line scale above anal origin deep, with deep alate tympanum, and deep pore [height/ length, 1.84 (1.54-2.23); tympanum height/length, .787 (.527-975); pore height/length, .324 (.250-.400)]. S. analis differs from S. michaelsarsi in that pigment on the pectoral fin, is limited only to the base, or to melanophores over the surface of the fin which may be individually distinguished, cf. pigment jet black, solid over entire fin (save five ventralmost rays), individual melanophores not readily discernible (in adults); 21-26 anal rays (usually 22-25) cf. 18-21 anal rays; 45-50 lateral line scales (usually 46-49) cf. 40-44 lateral line scales (usually 40-42); appressed pectoral fin reaching to pelvic insertion but not appreciably beyond, cf. appressed pectoral fin reaching past anal origin; caudal peduncle depth 6.3-8.6 per cent S.L. cf. 8.8-10.8 per cent S.L. S. analis differs from S. stephensi in that pectoral pigment may be limited to base or present on surface of fin, but is uniformly present over fin base or rays except ventralmost rays, cf. pigment on pectoral fin not present on base of fin, but limited to a patch of melanophores between second and sixth or seventh pectoral rays (counting from dorsal ray) and present on medial third of fin, not present at base or tip of fin; 21-26 anal rays (usually 22-25) cf. 20-22 (usually 20-21); 45-50 lateral line scales (usually 46-49), cf. 41-44; lateral line above anal origin relatively shallow with shallow tympanum and pore [H/L 1.33 (1.12-1.64); T/L .543 (.412-.685); P/L .233 (.176-.290)], cf. lateral line scale above anal origin deep, with deep alate tympanum and deep pore: H/L 1.86 (1.68-2.11); T/L .713 (.602-.810); P/L .302 (.260-.345). The characters used to distinguish Scopelarchus from other genera of scopelarchids will distinguish S. analis from all noncongeneric species of scopelarchids.

Description.—The description of S. analis is based on 474 (6.0-49.4) larval and metamorphic specimens and 128 (50.5-126.3) adolescent and adult specimens. With the exception of meristic characters the description based upon adults is given first, followed by an account of development.

MERISTIC CHARACTERS: Values in parentheses are those of the lectotype (data from Deckert, pers. comm.). Dorsal 7-9 (8); anal 21-26 (25); pectoral 18-22 (22); lateral line scales 45-50; vertebrae 44-49.

PROPORTIONAL DIMENSIONS: Based on 130 (28.4-126.3) specimens. Data taken from specimens from all oceans, specimens measured indicated by an asterisk (*) in listing of material examined. Expressed as thousandths of the standard length and given as the mean and range (in brackets).

A. Dorsal fin	7	8	9			
Form A	12	52	2			
candelops	6	103	7			
sagax		42	2			
B. Anal fin	21	22	23	24	25	26
Form A			3	32	26	5
candelops		24	37	52	10	
sagax	4	15	13	13	3	
C. Pectoral fin	18	19	20	21	22	
Form A		1	39	25	1	
candelops	10	47	53	13		
sagax		6	28	14		
D. Lateral line scales	45	46	47	48	49	50
Form A			7	30	26	2
candelops	1	15	17	23	6	
sagax	2	9	9	1		
E. Vertebrae	44	45	46	47	48	49
Form A			1		13	2
candelops	1	1	4	10	1	
sagax	1	2	3	1		

TABLE 7. Meristic comparison of forms of S. analis.

Body, depth at dorsal origin, 166 [142-228]. Caudal peduncle; least depth, 77 [63-86]; length, 143 [127-170]. Adipose fin: distance to midcaudal rays, 200 [169-222]; length of base, 42 [28-59]; length of fin 63 [41-74]. Anal fin: length of base, 280 [230-322]; length of longest ray, 106 [67-136]. Dorsal fin: length of base, 48 [34-61]; length of longest ray, 92 [65-128]; dorsal origin to anal origin, (distance between verticals), 225 [169-276]; end of dorsal base to base of midcaudal rays, 588 [539-635]. Pectoral fin, length of longest ray, 169 [116-210]. Pelvic fin, length of longest ray, 100 [71-137]. Pelvic insertion to anal origin, 160 [118-218]. Pectoral insertion to pelvic insertion, 197 [162-240]. Anus to anal origin, 50 [36-67]. Distance from snout to: anus, 558 [504-656]; dorsal origin, 393 [342-429]; anal origin, 599 [529-689]; pectoral insertion, 258 [232-290]; pelvic insertion, 442 [377-508]; orbit, 65 [52-78]. Head length, 233 [204-262]. Postorbital head length, 97 [78-117]. Orbit: horizontal diameter, 75 [55-89]; vertical diameter, 71 [51-87]. Interorbital width, 24 [10-49]. Upper jaw length, 168 [144-202]. Lower jaw length, 183 [162-227]. Longest dentary tooth, 38 [28-53].

BODY: Body depth 6.18 [4.81-8.90] in S.L. Peduncle depth 2.99 [2.62-3.96] in H.L. Peduncle length 1.61 [1.33-1.94] in H.L.

SKIN AND SCALES: Body scales moderate, those scales adjacent to lateral line scales less than one-third depth of lateral line scales. About five series of scales from lateral line to dorsal origin and about eight series from lateral line to anal origin. About 19-22 series from occiput to dorsal origin and about 36-40 series from dorsal origin to adipose fin origin.

Lateral line scales moderately large, numbering 45-50 in 148 specimens counted. Lateral line scale above anal origin based on 90 (29.6-126.3) specimens: H/L 1.33 [1.12-1.64]; T/L .543 [.412-.685]; P/L .233 [.176-.290]; tympanum small, nonalate, rounded or smoothly indented anteriorly, completely covering small central pore. Lateral line scale above pectoral insertion based on 19 (42.0-126.3) specimens: H/L 1.41 [1.13-1.58]; T/L .560 [.488-.614]; P/L .242 [.203-.274]; tympanum nonalate, small, usually smoothly indented at anterior margin. Penultimate lateral line scale based on 5 (65.1-94.5) specimens: H/L 1.35 [1.33-1.37]; T/L .584 [.527-.653]; P/L .314 [.289-368]. Ultimate lateral line scale based on 2 (91.0-94.5) specimens and listed in that order: H/L 1.11, 1.34; imperforate, circuli incomplete, no posterior field, reaching nearly to base of midcaudal rays.

HEAD: Eye diameter somewhat greater than snout length in adult specimens. Head length 4.33 [3.82-4.80] in S.L. Snout length 3.66 [3.10-4.24] in H.L. Horizontal eye diameter 3.05 [2.53-3.79] in H.L. Postorbital head length 2.41 [2.06-2.80] in H.L. Interorbital width 11.40 [5.00-25.00] in H.L.

Pectoral insertion opposite an indentation in opercle.

Pseudobranchiae well-developed. Counts: (41.6) 13; (65.5) 15, (68.4) 14, (81.9) 13, (94.5) 17. Gill filaments not extending to margin of gill cover. Gill membranes united below middle of eye.

MOUTH: Upper jaw length 1.39 [1.19-1.53] in H.L. Lower jaw length 1.25 [1.10-1.35] in H.L. Upper jaw extends from below posterior margin of eye to a distance about equal to lens diameter behind a vertical through posterior margin of eye in some specimens.

Tooth counts based on 6 [29.6, 41.6, 65.5, 68.4, 81.9, 94.5] specimens and listed in that order. Premaxillary tooth counts 23, 42, 52, 65, 90, 133. Dentary tooth counts lateral, 15, 20, 24, 24, 32, 33; medial, 6, 9,

9, 11, 12, 13. Longest dentary tooth 6.07 [4.50-5.58] of H.L. Palatine tooth counts 10, 12, 13, 13, 15, 17. Vomerine teeth small, one or (rarely) two per side. Lingual tooth counts 9, 12, 11, 11, 12, 15.

FINS: Dorsal moderate, longest dorsal ray 9.2 [6.5-12.8] per cent S.L.; length of dorsal base 4.8 [3.4-6.1] per cent S.L. Appressed pelvic fins reach nearly to anus but not to anal fin origin. Pelvic rays not as long as pectoral rays: length of longest pectoral ray 16.9 [11.6-21.0] per cent S.L., length of longest pelvic ray 10.0 [7.1-13.7] per cent S.L. Appressed pectoral fins reach nearly to or slightly beyond pelvic insertion but do not reach anus. Anal base short, 28.0 [23.0-32.2] per cent S.L.

COLOR: Dermal pigment on body limited to stripes dorsal and ventral to lateral line typical for species of *Scopelarchus*. Scale pockets edged with pigment dorsal but not ventral to lateral line. Caudal peduncle and scaly flaps of skin overlying bases of caudal rays well-pigmented. Three to four lines of pigment above and below midcaudal rays directed posteriad on membranes between caudal fin rays. Pigment lacking on anal and adipose fins. Dorsal fin pigmented at base and over entire fin except for last two rays. Pigment present on pectoral fin, at least at base of fin and usually on rays and membranes of fin as well. Pigment usually lacking but sometimes present on pelvic fins, never as well developed as on pectoral fins. Peritoneum dense black.

Development.—The description of development in S. analis is based on 392 (14.5-49.4) larvae and metamorphic specimens. Not included are 82 (6.0-12.5) specimens, mostly from the North Atlantic Central Water Mass area, that are tentatively associated with this species. Figure 50 illustrates in sequence the development of S. analis.

RECOGNITION: Larvae of *S. analis* can be distinguished from larvae of other scopelarchid genera through the following combination of characters (not all characters present in smaller individuals): dorsal 7-9 (usually 8); anal 21-26 (usually 22-25); pectoral 18-22 (usually 19-21); three peritoneal sections, an anterior unpaired section, and two posterior paired sections; pigment present on pectoral fin, but only in specimens larger than 22.0 mm. (usually not present in specimens smaller than 28-30 mm.); no accessory pigment areas or spots; two dermal pigment stripes, one dorsal and one ventral to lateral line as in all species of *Scopelarchus*.

Larvae of *S. guentheri* and *S. analis* are quite similar and can be easily confused, especially the smaller individuals. *S. analis* larvae 14.8-30.0 mm. in size can be distinguished from *S. guentheri* larvae of the same size through the following combination of characters: anal rays 21-26 (usually 25 or fewer), cf. anal rays 24-29 (usually 25 or more); head length greater





than 20 per cent S.L. (20.2-25.0), cf. head length usually less than 20 per cent S.L. (15.0-21.1); choroid pigment of eye not noticeably produced above lens, considerably smaller in size than pigment cup ventral to lens. not formed into a rounded cup, cf. choroid pigment of eve noticeably produced above eye (true for larvae 20-22 mm. or smaller in size), almost equal in size to pigment cup ventral to lens; formed into a rounded cup; dermal pigment appearing above anal base, well ahead of caudal peduncle, not present in specimens smaller than 19 mm.; pigmented area spreading anteriorly and posteriorly with growth, not extending to rear portion of caudal peduncle in specimens less than 25-29 mm, in size, cf. dermal pigment appearing as a spot on posterior portion of caudal peduncle in specimens 15-17 mm. in size, present in all specimens larger than 17 mm., pigmented area spreading anteriorly with growth but limited to caudal peduncle in specimens less than 25-28 mm. in size; pectoral fin pigment appearing as early as 22 mm., present in all specimens 30-35 mm. and larger, cf. pectoral fin pigment lacking in S. guentheri.

Two characters common to S. michaelsarsi and S. stephensi separate them easily from S. analis. Anal rays in S. analis 21-26 (usually 22 or more), cf. anal rays 18-22 (usually 21 or fewer); pigment lacking on caudal peduncle in specimens less than 25 mm. in size, cf. pigment present at rear of caudal peduncle in smallest known larvae [9.5 for S. michaelsarsi (Rofen, 1966e, p. 600) and 14.8 for S. stephensi] and in all larger specimens. Specimens of S. michaelsarsi and S. stephensi larger than 25 mm. have essentially full adult pigmentation (except for the peritoneum), while full adult pigmentation is not acquired in S. analis in specimens smaller than 30-35 mm., further it is possible to count lateral line scale pockets in specimens of S. michaelsarsi and S. stephensi [S. analis has 45 or more lateral line scales, S. stephensi and S. michaelsarsi have 44 or fewer] larger than 25 mm.

BODY: Body moderately short, moderately deep, with moderately deep peduncle. Head length greater than 20 per cent S.L. Snout length greatly exceeding eye diameter. Eye lacking rounded lobe of pigment over lens.

FINS: In the smallest positively identified specimens, 14.5-15.0 mm., only the caudal, dorsal, and anterior anal rays are ossified (or partly so) but it is possible to count the anal radials. This agrees well with Rofen (1966e, p. 581) who counted seven dorsal rays and 22 anal rays in his 13.1 mm. *S. candelops*, but was unable to count either fin in any larval *Scopelarchus* smaller than this (dorsal and anal rays are ossified by 12.0 mm. in my material of *S. michaelsarsi*). Pelvic fins appear as buds in ventro-lateral abdominal cavity wall at or below level of intestine beneath or behind posterior portion of dorsal base. Dorsal adipose fin extending to

over anterior one-third of anal base, but restricted in larvae over 20 mm. in size to adult proportions. Ventral adipose fin never larger than onehalf pelvic-anal distance in smallest larvae, considerably less than this in most, and reabsorbed in specimens larger than 22 mm. All fin rays ossified in specimens larger than 20-22 mm. Apparent order of ossification: caudal, dorsal, anal, dorsal pectoral, pelvic, ventral pectoral. Pelvics in larger specimens inserted beneath or behind posterior half of dorsal base.

PERITONEAL SECTIONS: Three peritoneal sections. Peritoneal pigment apparently developing a little later in growth than in other species of *Scopelarchus*, no specimen in my material smaller than 16.4 mm. has peritoneal pigment and specimens 17-20 mm. in size may have peritoneal pigment or not. Most specimens over 20 mm. in size have all three sections. Anterior peritoneal section appearing before posterior sections. Several larvae in my material have only the anterior section. However, most larvae of *S. analis* with peritoneal pigment have all three sections. Peritoneal sections expanding anteriorly, posteriorly, dorsolaterally and ventrolaterally with growth, eventually forming a complete tube around the gut in adults. Anterior and posterior sections fused over pelvic base in specimens larger than 50 mm.

DERMAL PIGMENTATION: Dermal pigmentation appears over the anal base in specimens 20 mm. and larger and consists of melanophores dorsal and ventral to the lateral line. Pigmented area expanding anteriorly and posteriorly with growth forming dermal stripes characteristic for the genus. Dermal pigmentation lacking from rear portion of caudal peduncle in specimens smaller than 25-30 mm. Pigmentation on head, particularly on snout and occiput, appearing in specimens 26-30 mm.

GUT: Postpelvic gut length never less than one-half pelvic-anal distance, usually considerably more than this. Anus reaching adult position, just anterior to anal origin, in specimens 20-22 mm. Rearward expansion of caecum first evident in specimens 24-28 mm., reaching slightly beyond pelvic insertion in specimens 36-40 mm.

METAMORPHOSIS: Completion of metamorphosis defined as point of fusion of anterior and posterior peritoneal sections over or just before pelvic base with concomitant rearward expansion of caecum (to just before anus in adults). This occurs in specimens 45-55 mm. in size in *S. analis*, and 50 mm. is rather arbitrarily taken as the dividing line between metamorphic and adult specimens.

Discussion.—Five different specific names have been proposed based on specimens of this species: S. analis (Brauer), S. beebei Rofen, S. candelops Rofen, S. perarmatus (Roule), and S. sagax Rofen. Rofen (1966e) recognized all five, having described three of them himself. Delaying for the moment consideration of S. beebei, a species based only on larval material, Rofen (1966e, p. 582) claimed that S. candelops differed from S. perarmatus as follows: palatine teeth not entering profile when mouth is open, cf. markedly entering profile; angle of gape before eve to middle of eve when mouth is nearly closed, cf. near posterior edge of eve in S. perarmatus. The first statement must in part be based on Roule's (1919, plate 5, fig. 2 + 2A) figure for I find in most specimens the anterior palatine teeth may or may not slightly enter the profile formed by the upper jaw, but find no differences in this respect among all my adult material of S. analis. I further find for my material that when the mouth is closed the angle of the gape extends from beneath the middle of the eye to the posterior edge of the eye, but again find no consistent differences in this respect. S. perarmatus was said to differ from S. candelops and S. sagax in the form of the eve: lens smaller and pearl organ more prominently developed in S. candelops and S. sagax. This statement again must have been based on Roule's figure, which is somewhat inaccurate in depicting the eye as well as in other respects. In any case, this difference again is not recognizable in my material, the size of the eye and development of the pearl organ being about the same for all specimens of comparable size. Roule's (1916, 1919) description and his figure are sufficient to establish his specimens, at least the one specimen figured, as S. analis. The counts (dorsal 7, anal 25, pectoral 19), the indicated size of the lateral line scales (1919, plate 5, fig. 2), the color pattern ("spots of color along the lateral line"), and the position and relative size of the fins, and the capture of these specimens in the Eastern North Atlantic, east of the Azores, leave little doubt that Roule's specimens belong to the species described by Brauer.

Both S. candelops and S. sagax were said by Rofen (1966e, pp. 582, 589) to differ markedly in color pattern from S. analis. Rofen did not amplify this statement for S. candelops but S. sagax was said to differ from S. analis as follows: few or no external chromatophores on body anterior to caudal peduncle vs. extensive pigmentation along entire lower side of body; coloration before upper anterior edge of eye absent vs. present; pearl organ elongate horizontally cf. vertically. All three statements are obviously based on Brauer's (1906, plate 10, figs. 1, 2) figures of S. analis, which are inaccurate. First, the smaller specimen depicted in Figure 2 is not S. analis. From the enlargement size given (6:1) 1 have calculated this specimen to be roughly 18 mm. S.L. If so, the specimen is S. guentheri, the combination of an enlarged spot of pigment on the caudal peduncle, lack of dermal stripes along the lateral line, incomplete development of fin rays, and presence of an expanded

lobe of choroid pigment over the eye, being distinctive for this species at this size. I have not included this specimen in the synonymy of S. guentheri for the simple reason that Brauer did not identify the station from which it came, did not specify its length, and both figures are somewhat inaccurate, leaving the identification open to some doubt. As for the reputed differences between S. sagax and S. analis, they are obviously based on inaccuracies in Brauer's Figure 1. No species of Scopelarchus has extensive pigmentation along the entire lower side of the body, but the major pigment pattern represented in Brauer's figure, i.e., dermal stripes dorsal and ventral to the lateral line is true for all species of Scopelarchus. No species of Scopelarchus has a bar of pigment bordering the anterior edge of the eve (cf. Scopelarchoides signifier, S. danae, etc.) but all have pigment on the snout. Finally, no known scopelarchid has the pearl organ elongate in the vertical dimension as depicted in Brauer's figure. Other differences between S. sagax and S. analis were said to be as follows (Rofen, 1966e, p. 589): lower jaw curved vs. straight; anal rays 22-23, cf. 25. The lower jaw is curved in all species of Scopelarchus whereas the range of anal fin rays indicated, 22-25, includes 96 per cent (228/237) of the specimens of S. analis counted (total range for the species is 21-26, see Tables 2, 7). Thus I can find no basis, either in Rofen's characters, nor in examination of in excess of 600 specimens of this species for separating S. candelops or S. sagax from either S. perarmatus or S. analis.

S. beebei (Rofen, 1963, 1966e) was based on 3 [9.8, 20.4, 22.1] specimens. Rofen's (1966e, p. 593) illustration of the smaller specimen, 9.8 mm., as well as his description, convince me that this is a specimen of S. michaelsarsi. I have never seen peritoneal pigment in S. analis in specimens smaller than 16.4 mm.

The characters used by Rofen (1966e, pp. 590, 593) to distinguish *S. beebei* are a mixture of characters common to the genus or to the family and characters distinctive for *S. analis. S. beebei* was said to be different in possessing an elongate snout, this so far as I know is true for all larval scopelarchids at comparable stages of development. *S. beebei* was said to be different in having the pelvic fin insertion well behind the dorsal base. This is true for most *Scopelarchus* larvae, although in all four species the point of insertion varies from beneath the posterior half of the dorsal base to behind the dorsal base. Finally, *S. beebei* was said to be distinctive in having no body pigmentation other than that of the eye and peritoneal sections and in having 22-23 anal rays. These latter characters positively establish *S. beebei* as a synonym of *S. analis*.

A few comments on Rofen's smaller larval material and particularly his key (1966e, p. 570) to postlarvae of scopelarchids of the western North Atlantic are in order before turning to consideration of S. candelops and S. sagax. I tentatively agree with Rofen's (1966e, pp. 580-581), identification of the four smallest larve of S. candalops (= S. analis). 8.8, 9.0, 10.2, 11.0, which were said to lack dermal pigmentation and peritoneal sections. However, these larvae also lacked ossified fin rays or radials and, in the absence of other diagnostic characters, the identification is open to some doubt. I reject Rofen's identification of the three smallest specimens of S. sagax (= S. analis) 3.9, 4.1, 4.9, which were said to have a large head and relatively short body, anus at about midlength, no formed fin rays, pigmentation consisting of a chromatophore on each side of anus, a pigment cell ventrally at base of anal finfold equidistant between anus and tip of hypural fan, and two chromatophores on dorsum each slightly behind verticals from respective ventral pigment spots; heart pigmented; pectoral fin with pigmentation near upper edge; head pigmented on tips of jaw, base of cranium, and upper posterior rim of orbit; fine lines of brown coloration along lower edges of isthmus, pectoral girdle and suspensorium, eye compressed, large lens directed forward; no evident teeth. Although the description superficially corresponds in some respects to larvae of *Rosenblattichthys*, it is, in fact, enough to establish that these specimens are not scopelarchids, at least any known scopelarchids. I have examined the three specimens in question, but they are so mutilated as to preclude identification, to family or order. The remaining material of S. sagax consisted of specimens 26.3 mm. and larger and, indeed, as pointed out below, this would have to be the case since no S. analis larva could be assigned to S. sagax until pectoral fin pigment had developed. The key to postlarvae (Rofen, 1966e, p. 570) distinguishes six entities. The form identified as possibly a species of Benthalbella could be B. infans, which occurs in the Western North Atlantic, but cannot positively be identified from the information presented. The other dichotomies are based mostly on Rofen's lack of an adequate series of larvae. The series of dichotomies separating S. beebei, S. candelops, and S. sagax are all based on differences in the size of material examined to formulate the key: S. candelops based on 5 (8.8-13.1), S. beebei on [9.8, probably = S. michaelsarsi + 2 (20.4-22.1) clearly = S. analis], 3 S. sagax [3(3.9-4.9), not scopelarchids + 11 (26.3-126.6)]. The difference between Phanops (= Scopelarchus) michaelsarsi and Scopelarchus sp. is strictly developmental; both are S. michaelsarsi.

Finally, *Scopelarchus candelops* was said to differ from *S. sagax* in the following characters:

1. Two pores medial to nostril, cf. three medial to nostril in *S. sagax*. There are three pores situated over the nasal bone medial to each nostril in all known species of scopelarchids.

2. Dark pigment at upper anterior rim of eye, cf. none in S. sagax. This is not true for any known species of Scopelarchus.

3. One row of gill teeth on each plate, cf. two to three rows in *S. sagax.* Neither this difference nor the difference in actual number of bases (Rofen, 1966e, 579) holds up under examination. There are specimens conforming in pectoral pigment with *S. candelops* having two to three rows per plate and the reverse is also true. As mentioned in the osteology section above, 1 mistrust any character having to do with the gill teeth or gill tooth plates. The number of rows per plate, the number of teeth per row, and the number of plates vary in a nonuniform fashion ontogenetically.

4. Tympanum of lateral line scale over pectoral fin base rounded or truncate cf. indented at its anterior margin in S. sagax. Rofen (1966e, p. 583) himself pointed out that this does not always hold, for he found a lateral line scale in the holotype of S. candelops with an indented anterior margin on the tympanum, but claimed (footnote 14) "... this exception must be rare." In fact, based on examination of the lateral line scales above the pectoral base of 19 (42.0-126.3) specimens, I find the tympanum to be usually smoothly but shallowly indented, but ranging from truncate to rather deeply indented in specimens agreeing in other characters with either S. candelops or S. sagax.

5. Large breast scale behind pectoral insertion deeply notched almost to focus, cf. rounded or slightly notched on anterior margin in *S. sagax*. Again Rofen (1966e, p. 583, footnote 15) points out an exception in that one specimen of *S. sagax* was found to have a deeply notched breast scale as in *S. candelops*. Such a notch is, however, an artifact. I have produced a deeply notched scale corresponding to Rofen's (1966e, p. 577) figure from an unnotched scale on several occasions by accidently flexing it during examination. I have never found an undamaged scale in *S. analis* to be as deeply notched as Rofen indicated.

6. Two peritoneal sections narrowly divided over ventral fins, cf. three in juveniles of S. sagax. Here Rofen included the posterior paired peritoneal sections as one. This statement is simply not true for any scopelarchid I have seen, and is probably based on the mistaken identification of the fusion of the anterior peritoneal section with growth with a third (fourth in my terminology) independent peritoneal sections.

7. Pectoral fins colorless or having fine pigmentation along rays but not on the membranes, cf. pigmentation on the rays and membranes. This is the only character provided by Rofen that actually varies enough that specimens could actually be separated on the basis of it. In fact, pectoral fin pigment ranges from none at all (all specimens smaller than 22.0 mm., all but three specimens smaller than 28 mm.) to present only at the bases of the fin rays, to developed in longitudinal lines along the fin associated mostly with the fin rays, to pigmentation extensively developed over the fin rays and membranes, covering the entire fin except the ventralmost five rays. As this is the only character provided by Rofen that will separate specimens. I divided my specimens of S. analis at first into two groups, one with extensive pigment over the entire fin. covering both rays and membranes, and the other group with specimens having pigmentation on the pectoral fin less well developed than this. This technique, of course, is somewhat arbitrary, and a subjective decision as to how extensive "extensive pigmentation" had to be was made in some cases. In any case, the two groups consisted of 125 (22.0-126.3) specimens with extensive pigmentation and 474 (6.0-113.2) with less extensive pigment, the latter, of course, including all larvae lacking pigment. The first group was later separated into two groups, based mainly on differences in meristic characters (table 7), one group 65 (48.5-68.0) termed form A and one group 59 [52 (22.0-48.4) + 7 (50.5-126.3)] termed "sagax." The larger group with 474 specimens was termed "candelops." Using this terminology it can be seen that "sagax" and "candelops" cooccur almost everywhere (the triangles and open circles, respectively, in Figure 51), whereas form A (the squares) is limited to the eastern North Atlantic.

These three groups of specimens were treated separately for purposes of acquisition and analysis of data. Meristic comparisons between the three groups are presented in Table 7. Lateral line scales (over anal origin) were measured from 37 (54.7-68.0) specimens of form A; 43 (29.6-95.0) specimens of "candelops;" and 10 (38.5-126.3) specimens of "sagax" based on specimens throughout the range of the species. Measurements of 31 characters were obtained from 20 (48.5-65.5) specimens of form A; 40 (28.4-113.2) specimens of candelops; and 25 (28.5-126.3) "sagax;" the latter two from throughout the range of S. analis.

Form A (table 7) differs from "candelops" and "sagax" in having a higher average number of anal rays, lateral line scales, and vertebrae. I view this as a probable effect of environmental temperature (see Barlow, 1961). No differences in the shape or proportions of the lateral line scales were found. The ranges of the proportions (expressed as thousandths of the S.L.) overlapped completely, although small but statistically significant differences between the means were found for a number of characters. However, in nearly all cases the differences were between form A and "sagax" (measurements of form A were based only on adults, 54.7-65.5 except for the 48.5 mm. specimen; whereas "sagax" is known from only





seven adults, and the measurements were based mainly on individuals 28-40 mm. in size) with the mean values for "candelops" intermediate, and the range of values for "candelops" completely overlapping the range of values for form A and "sagax." I have been unable to find any differences in pigmentation, larval morphology, or other characters. I conclude that S. candelops and S. sagax are synonyms, and that both are synonyms of S. analis.

Distribution.—Scopelarchus analis is a circumglobal warm-water species, occurring throughout the North Atlantic, South Atlantic, Indian Oceans (south of the equator), western and central Pacific (but apparently excluded from Pacific Equatorial Water) and off California and Baja California in the eastern Pacific (fig. 52).

Larvae of this species have been taken throughout the year in all areas. Larvae have frequently been taken in hauls restricted to the upper 100 m., and have been taken in numerous hauls within the upper 30-50 m. Adults have been taken in hauls to depths of 300 m. or more and most adults have been taken in hauls to 500 m. or more. Only three hauls to depths less than 300 m. all at night, have captured adults of this species (0-190 m., 0-250 m., 0-275 m.). S. analis is one of the few scopelarchids to have been taken in closing gear. Nybelin (1948, p. 40) reported three (8.5-26.0) specimens from a haul in the eastern North Atlantic with a 2 m. ring-net, fished and closed with 800 mwo. Harisson (1967, p. 78) reported four specimens of "S. guentheri" from three different hauls with an IKMT using a catch dividing bucket, taken in the Canary Basin, two specimens, daytime (760-600 m.); two specimens, nighttime, one from a haul 800-600 m., one from a haul 400-0 m. No sizes were recorded.

Material examined.—A total of 602 (6.0-126.3) specimens from 275 collections. In the listing of material examined the following abbreviations are used: (*) = specimen(s) measured; (A) = form A; (S) = "S. sagax"; all specimens not denoted by A or S are referred to "S. candelops." Paratypes. S. candelops. USNM 100514, 1 (35.1). S. sagax. NYZS (now deposited at CAS): 9698, 1 (34.0*). 10016, 1 (29.8*). 10417, 1 (33.1*). 16131, I (26.0). 18347, 1 (126.3*). 22116, 1 (35.0*).

North Atlantic. DANA: D1157 V, I (81.9*). D1159 V, (55.5*). D1162 II, I (63.2*). D1165 1X, 1 (39.4*)S. D1180 1, 1 (31.0*)S. D1181 V, 1 (45.5*). D1188 11, 1 (53.5*). D1189 V, I (36.0*). D1190 1, 1 (27.5). D1214 III, 1 (18.5). D1215 V, I (19.0). D1223 II, 1 (24.0). D1238 1, 1 (32.6*). D1269 VIII, 1 (29.6*). D1291 1, 1 (65.5*). D1291 III, I (32.5). D1337 V, 2 (42.1*-51.1*). D1339 1, 1 (43.4). D1369 II, 1 (56.5*)A. D1372 I, 4 (57.1-65.1)A. D1374 1, 7 (58.2-63.0/62.7*)A. D1374 VIII, 7 (58.0-64.4/ all 7 measured)A. D1374 1X, 1 (62.3)A. D1377 1, 20 [57.7-68.0/4 (60.6-65.5)*]A. D1377 II, 5 (61.5-63.9)A. D1377 III, 4 (58.0-61.0)A. D1377 VIII, 9 [56.5-64.0/ 4 (61.0-63.0)*]A. D1377 1X, 3 (60.0-61.4)A. D1379 I, 1 (62.4) A. D1380 I, 3 [55.5-64.0/ 2 (55.5-59.6)*]A. D4001 II, 1 (57.5*). D4003 VI, 1 (20.5). D4003 VIII, 1 (33.5)S. D4003 XI, 15 (15.0-25.5). D4004 III, I (32.5)S. D4004 IV, 5 (18.4-23.1). D4004 V, 3 (17.1-24.1). D4005 I, 1 (43.6*)S. D4005 VIII, 1 (23.0). D4005 IX, 2 (15.1-21.9). D4005 X, 10 (12.2-24.6). D4005 XI, 1 (20.0). D4006 II, 1 (18.6). D4006 III, 1 (32.0)S. D4006




1V. 17 (18.0-26.0). D4006 V. 5 (21.1-27.1). D4007 11, 2 (35.0*-36.5*)S. D4007 111, 2 (34.0*-36.4*)S. D4007 IV. 1 (20.1). D4007 V. 1 (28.0). D4009 II. 1 (38.9*). D4010 III. 2 (38.5-42.0)S. D4010 IV. 1 (22.9). D4014 III. 1 (20.4). D4014 IV. 1 (43.0). D4017 IV. 4 (6.0-25.5). D4017 V, 1 (23.0), D4017 VI, 5 (15.1-42.6), D4017 VII, 1 (37.5), D4017 VIII, 39 (9.6-46.5), D4017 1X, 2 (9.5-20.5). D4018 11, 2 (12.0-24.1). D4018 111, 4 (15.9-39.1). D4018 IV, 1 (21.6). D4019 111, 1 (25.2). D4019 V111, 6 (7,1-22.9). D4023 V, 6 (19.4-26.5). D4023 IX, 6 (16.1-25.5). D4023 X, 1 (24.0). D4023 XIII, 2 (21.5-24.8). D4023 XV, 2 (21.0-26.5). D4141 I, 4 (18.9-24.5). D4141 11, 1 (27.1). D4147 1, 3 (25.0-29.0). D4147 11, 6 (18.0-27.8). D4147 VIII, 1 (35.1). D4147 1X, 1 (24.5). D4157 111, 1 (48.5*)A. D4197 V11, 1 (20.0)A?. D4195 111, 1 (27.5). THOR 231, 1 (42.7*). ISH: ISH 153, 2 (60.0*-69.1*). ISH 383, 1 (71.6*). ISH 478, 1 (106.8). ISH 532, 1 (88.4*), 1SH 635, 2 (92.0-93.4), 1SH 2287, 1 (57.5), 1SH 2624, 1 (96.4), 1SH 3021, 1 (74.8)S. USNM, ACRE: 1-11B, 1 (17). 1-16A, 1 (19.5). 1-20A-D, 1 (21.0). 2-2, 1 (27.0). 2-4, 1 (19.4). 2-6, 1 (41.6*). 3-1, 1 (29.5)S. 3-5, 1 (23.5). 3-6, 1 (16.6). 3-6, 2 (22.5-26.5). 3-7, 2 (23,5-24,8), 3-10, 1 (30,0*)S, 3-13, 1 (21,5), 3-13, 1 (16,2), 3-14, 1 (22,0), 3-14, 1 (14,5), 4-5B, 2 (24.9-27.0). 4-5C, 1 (28.1). 4-10A, 2 (26.1-30.5*). 4-16C, 1 (29.5)S. 4-19B. 2 (17.0-19.5). 4-21C, 1 (40.1*). 4-21C, 1 (24.5). 4-25C, 1 (31.5). 4-27A, 1 (24.2). 4-31, 1 (23.9). 4-31, 1 (16.5). 6-2A, 1 (25.5). 6-8C+D, 1 (40.1*)S. 6-10C+D, 1 (34.0*)S. 7-12, 1 (25.4). 8-1C+D, 1 (21.8). 8-2, 1 (14.6). 9-2B, 1 (18.6). 9-7, 1 (25.9). 9-15, 1 (30.0)S. 9-19, 1 (30.6). 9-19, 1 (31.2)S. 9-24, 2 (32.5-32.9)S. 9-27, 1 (48.6), 9-27, 1 (38.9)S. 10-2B, 1 (22.1), 10-2C, 1 (16.9), 10-3C, 1 (26.4), 10-4B, 1 (42.4), 10-11B, 1 (36.0), 10-15B, 1 (18.6), 10-15C, 1 (22.1), 10-15C, 1 (21.5). 10-16C, 1 (35.0). 10-19A, 1 (48.4)S. 10-21N, 1 (70.1)S. 10-29M, 1 (35.0)S. 11-1B, 1 (27.1). 11-1M, 1 (21.0). 11-3B, 1 (14.1). 11-5B, 1 (20.5). 11-5M, 1 (19.9). 11-8C, 3 (16.9-21.0). 11-8C, 1 (22.9). 11-10C, 1 (1%]1(] WHOI RHB collection numbers: 1263, 9 (21.9-27.5). 1269, 1 (32.9)S. 1288, 2 (17.4-22.0). 1294, 5 (19.5-25.0). 1294, 9 (11.0-24.0). 1297, 3 (18.0-19.0), 1301, 1 (43.6), 1302, 2 (54.5-60.0), 1303, 15 (15.0-22.0), 1306, 1 (35.5), 1307, 8 (12.5-27.0). 1314, 2 (23.0-29.0).

South Atlantic. DANA: D3979 11, 2 (22.1-31.2). D3980 11, 1 (33.5). D3981 111, 3 (34.5-42.0)S. D3996 1, 1 (113.2*). D3996 11, 1 (41.0*)S. D3996 111, (47.2*)S. D3996 V111, 1 (40.0*)S. D3997 11, 1 (33.9)S. D3999 11, 1 (50.5*)S. D4000 11, 2 (12.1-25.8). D4000 111, 8 (8.6-12.4) + 1 (32.3*)S. ISH: ISH 590, 1 (54.1*). ISH 590, 1 (45.2*)S. ISH 723, 1 (47.8*)S. ISH 1361, 1 (47.5). ISH 1485, 1 (78.9). ISH 2165, 2 (66.2-74.5). ISH 2218, 1 (91.4). ISH Walther Herwig Station 4091/71, 1 (61.5)S.

Indian Ocean. DANA: D3804 111, 3 (15.6-22.1). D3849 I, 2 (16.8-21.4). D3941 I, 2 (22.0-23.4)S. D3964 11, 1 (28.5*)S. D3969 111, 1 (30.0). D3971 11, 1 (23.0). SOSC: E 35-2281, 1 (43.9)S. USNM: AB 3-22, 1 (81.5). AB 3-23, 1 (84.5). AB 6-344A, 1 (24.2). AB 6-341D, 2 (78.1-82.1).

Western Pacific. DANA: D3680 V1, 1 (91.5*)S. D3739 11, 2 (35.5-66.9). D3739 1X, 1 (45.3). D3749 1, 2 (85.4*-85.6*). D3767 V, 1 (91.0*). D3791 11, 9 (14.5-23.1). D3800 11, 9 (28.5-44.5). D3971 11, 1 (31.0)S. SIO: SIO61-544, 18 (14.6-22.0). SIO69-20, 1 (32.2). SIO70-306, 1 (31.0)S. SIO70-311, 3 (28.0-41.5). SIO70-334, 1 (32.6).

Central South Pacific. DANA: D36241, 1 (56.6*). SIO: S1O69-348, 3 (14.8-22.6). S1O70-109, 1 (25.5). S1O70-119, 1 (28.4). SIO, uncat. Climax 11 117-7, 2 (18.6-19.0). USNM, *Eltanin* stations: E31-15A, 1 (85.0*)S. E31-21A, 1 (28.5). E31-25A, 1 (24.1). SOSC, *Eltanin* 35-2280, 1 (27.1).

Eastern South Pacific. WHOI: AB 13-26, 1 (59.5). AB 13-30, 1 (29.2).

Central North Pacific. DANA: D4771, 1 (33.0). D4812, 1 (28.3).

NMFS: HMS 27-28, 2 (17.1-26.6). HMS 27-49, 1 (21.5). HMS 32-31, 1 (34.5). HMS 32-47, 1 (21.8). HMS 37-42, 1 (17.0). JRM 21-2, 1 (15.6). SIO: SIO60-251, 1 (44.5). SIO60-

285, 1 (76.0). S1O61-48, 1 (60.5). S1O68-471, 1 (51.6*). UH: 69/9/25, 1 (82.6*). 69/9/27, 1 (89.0). 69/11/1, 5 (22.5-59.5/59.5*). 69/11/3, 1 (30.5). 69/11/6, 2 (28.4*-31.5). 69/11/8, 1 (26.9). 69/11/9, 1 (32.7). 69/11/11, 1(49.4*). 70/6/6, 1 (33.0)S. 70/7/16, 2 (15.0-19.1). 70/7/24, 1 (94.5). 70/7/25, 1 (22.1). 70/7/26, 4 (16.5-20.0). 70/7/27, 1 (68.4). 70/7/28, 1 (25.2). 70/7/32, 1 (22.0). 70/9/8, 10 (17.5-21.5). 70/9/9, 1 (16.5). 70/9/12, 2 (92.0-95.0). 70/9/13, 1 (84.6). 70/9/24, 3 (87.3-91.0). 70/9/28, 5 (15.9-18.3). 70/9/29, 1 (90.1)

Eastern North Pacific. LACM: LACM 9366, 1 (31.0). LACM 9408, 1 (81.4*). LACM 9564, 1 (22.6). LACM 9686, 1 (33.5). LACM 9674, 1 (41.6*). LACM 9701, 3 (29.0-35.1). OSU: OSU 560, 1 (mutilated). OSU 561-562, 1 (77.5*). SIO: SIO55-204, 1 (53.0*). SIO63-409, 1 (19.5). SIO63-423, 1 (25.1). SIO65-193, 1 (33.8). SIO66-31, 1 (20.2). SIO70-21, (30.0). SIO70-95, 1 (33.5). SIO70-238, 1 (37.2). USC - V 12716, 1 (65.5*).

Scopelarchus guentheri Alcock 1896. Figure 53.

Scopelarchus guentheri Alcock, 1896, pp. 306-308; 1897, pt. IV, pl. XVIII, fig. 7; 1899, pp. 152-153. Parr, 1928, p. 159; 1929, p. 12. Norman, 1937, p. 86. Maul, 1946, p. 17. Nybelin, 1948, p. 42. Mead and Bohlke, 1953, p. 244. Marshall, 1955, pp. 307-315 (in part). Andriashev, 1960, pp. 565-566. Rofen, 1963, pp. 1-4. Misra and Menon, 1966, p. 428. Kotthaus, 1967, pp. 83-84. McAllister, 1968, p. 95. Craddock and Mead, 1970, p. 3.26 (in part).

Questionable references: Bertelsen and Marshall, 1956, p. 13. Backus et al., 1965, p. 145. Berry and Perkins, 1966, p. 667. Harrisson, 1967, p. 78.

Holotype.—Ca. 127 mm. S.L. (5 in.). R.I.M.S. Investigator off Indus Delta, 22° 14.4' N, 67° 08.9' E. Deposited in Indian Museum, Calcutta.

Comparative diagnosis.—A species of Scopelarchus with 7-8 dorsal rays, 24-29 anal rays, 18-21 pectoral rays, and 47-52 lateral line scales. S. guentheri is distinguished from S. analis in the diagnosis of that species. S. guentheri is distinguished from S. michaelsarsi and S. stephensi in lacking pigment on the pectoral fin, in having 24 or more anal rays, cf. 22 or fewer, and in having 47 or more lateral line scales, cf. 44 or fewer.

Description.—Based on 121 (14.8-49.5) larvae and metamorphosing specimens and 66 (50.0-119.0) adolescent and adult specimens. With the exception of meristic characters, the description given first is that based upon adults, followed by an account of development.

MERISTIC CHARACTERS: Values in parentheses are those of the holotype (taken from Alcock, 1896, pp. 306-308). Dorsal 7-8 (9, Alcock probably counted the last divided ray as two separate elements); anal 24-29 (26, last divided ray may have been counted as two by Alcock), [(102/107 (or 95.4 per cent) have anal = 25-28]; pectoral 18-21 (19) [see discussion, all *S. guentheri* have 18 or 19 pectoral rays except specimens taken in transitional waters of the eastern Pacific or in the subtropical convergence] lateral line scales 47-52 (50); vertebrae 47-51.

PROPORTIONAL DIMENSIONS: Based on 33 (33.0-112.4) specimens



Fig. 53. Scopelarchus guentheri Alcock. A. Adult, DANA 3904 I, 96.0. B. Lateral line scale above anal origin, DANA 11781I, 54.5. C. Lateral line scale above pectoral insertion, DANA 3828 XIII, 88.5. D. Penultimate lateral line scale, ORSTOM CYCLONE V-1, 97.0. (data taken from specimens from all oceans. Expressed as thousandths of the standard length and given as the mean and range (in brackets).

Body, depth at dorsal origin, 142 [108-174]. Caudal peduncle: least depth, 70 [55-76]; length, 137 [112-158]. Adipose fin: distance to midcaudal rays, 199 [183-218]; length of base, 38 [27-52]; length of fin, 57 [38-74]. Anal fin: length of base, 306 [258-352]; length of longest ray, 100 [76-131]. Dorsal fin: length of base, 39 [30-44]; length of longest ray, 70 [51-117]; dorsal origin to anal origin (distance between verticals), 216 [189-254]; end of dorsal base to base of midcaudal rays, 610 [575-642]. Pectoral fin, length of longest ray, 180 [145-222]. Pelvic fin, length of longest ray, 99 [78-140]. Pelvic insertion to anal origin. 154 [125-176]. Pectoral insertion to pelvic insertion, 187 [177-204]. Anus to anal origin, 56 [38-83]. Distance from snout to: anus, 532 [496-592]; dorsal origin, 363 [338-390]; anal origin, 580 [554-641]; pectoral insertion, 243 [216-282]; pelvic insertion, 408 [377-478]; orbit, 53 [46-63]. Head length, 212 [183-233]. Postorbital head length, 93 [79-106]. Orbit: horizontal diameter, 73 [59-87]; vertical diameter, 69 [55-82]. Interorbital width, 18 [10-27]. Upper jaw length, 149 [136-173]. Lower jaw length, 161 [150-188]. Longest dentary tooth, 33 [21-41].

BODY: Body depth 6.96 [5.74-9.29] in S.L. Peduncle depth 3.10 [2.72-3.81] in H.L. Peduncle length 1.65 [1.47-1.92] in H.L.

SKIN AND SCALES: Body scales moderate, those scales adjacent to lateral line less than one-fifth depth of lateral line scales. About four series of scales from lateral line to dorsal origin and five or six series from lateral line to anal origin. About 20 series of scales from occiput to dorsal origin and 38-40 from dorsal origin to adipose fin origin.

Lateral line scales large, numbering 47-52 in 46 specimens counted. Lateral line scale above anal origin based on 50 [33.0-112.4] specimens from throughout the range of the species: H/L 1.84 [1.54-2.23]; T/L.787 [.527-.975]; P/L .324 [.250-.400]; tympanum extremely deep, alate, rounded or very slightly indented anteriorly, completely covering large central pore. Lateral line scale above pectoral insertion based on 3 [88.5 (Indian Ocean), 102.5 (Central North Pacific), 112.4 (Western Pacific)] specimens and listed in that order: H/L 1.51, 1.33, 1.49, T/L .744, .565, .610; P/L .292, .298, .248; tympanum alate, completely covering large central pore. Penultimate lateral line scale based on 4 [94.5, 97.0, 102.5, 112.4] specimens and listed in that order [Western Pacific, 2 (97.0-112.4); Central North Pacific, 1 (102.5); no available data, but from either Western or Central Equatorial Pacific, 1 (94.5)]: H/L1.65, 1.65, 1.94, 1.58; T/L .750, .785, .980, .646; P/L .350, .292, .377, .323. Ultimate lateral line scale, based on 2 [Western Pacific, one (97.0), Central North Pacific, 1 (102.5)] specimens and listed in that order: H/L 1.30, 1.80; imperforate, circuli incomplete, no posterior field.

HEAD: Eye diameter noticeably greater than snout length. Head length 4.68 [4.30-5.46] in S.L. Snout length 4.03 [3.59-4.42] in H.L. Horizontal eye diameter 3.01 [2.53-3.80] in H.L. Postorbital head length 2.31 [2.14-2.74] in H.L. Interorbital width 13.86 [8.46-21.80] in H.L.

Pseudobranchiae well-developed. Counts: (42.5) 9; (58.0) 10; (70.2) 11; (102.5) 14. Gill filaments rather elongate extending to or beyond edge of gill covers. Gill membranes united below anterior margin of eye.

MOUTII: Upper jaw extends to a point slightly before to slightly behind vertical through posterior margin of eye. Upper jaw length 1.43 [1.33-1.52] in H.L. Lower jaw length 1.32 [1.23-1.44] in H.L. Tooth counts based on 4 (42.5, 58.0, 70.2, 102.5) specimens and listed in that order: Premaxillary tooth counts: 28, 37, 61, 81. Dentary tooth counts: lateral, 14, 16, 25, 25; medial, 7, 9, 11, 18. Longest dentary tooth 6.57 [5.27-11.90] in H.L. Palatine tooth counts: 9, 11, 14, 14. Lingual tooth counts: 8, 11, 11, 13.

FINS: Dorsal moderate, longest dorsal ray 3.9 [3.0-4.4] per cent S.L.; length of dorsal base 7.0 [5.1-11.7] per cent S.L. Appressed pelvics reach anus but not anal fin origin. Pelvic rays not as long as pectoral rays: length of longest pectoral ray 18.0 [14.5-22.2] per cent S.L., length of longest pelvic ray 9.9 [7.8-14.0] per cent S.L. Appressed pelvic fins reach past pelvic insertion but do not reach anus. Anal base elongate, 30.6 [25.8-35.2] per cent S.L.

COLOR: Dermal pigment on body limited to stripes dorsal and ventral to lateral line typical for species of *Scopelarchus*. Scale pockets edged with pigment above but not below lateral line. Caudal peduncle and scaly flaps of skin overlying bases of caudal rays densely pigmented. Pigment lacking on pectoral, pelvic, anal, adipose, and caudal fins. Pigment present at base and on rays and membranes of dorsal fin. Peritoneum dense black.

Development.—The description of development in S. guentheri is based on 12 (14.8-49.5) larvae and metamorphic specimens. Not included are 18 (7.0-17.1) specimens tentatively associated with this species, but lacking all distinguishing characters save the shape of the layer of choroid pigment in the eye (see below). Figure 54 illustrates in sequence the development of S. guentheri.

RECOGNITION: Larvae of *S. guentheri* can be distinguished from larvae of other scopelarchid genera through the following combination of characters: dorsal 7-8, anal 24-29 (usually 25-28), pectoral 18-21 (usually 18-19, see "Discussion"); three peritoneal sections, an anterior un-





paired section, and two posterior paired sections; pigment lacking on pectoral fin; no accessory pigment areas or spots; dermal pigment develops as two stripes dorsal and ventral to lateral line as in all species of *Scopelarchus*.

Larvae of *S. guentheri* can easily be distinguished from those of *S. michaelsarsi* and *S. stephensi* in having more anal rays, 24-29, cf. 22 or fewer.

The larvae of *S. guentheri* and *S. analis* are quite similar and can easily be confused. The larvae of these two species are distinguished in the description of the larvae of *S. analis*.

BODY: Body elongate, shallow, with shallow peduncle, least depth 7.6 per cent S.L. or less. Head usually less than one-fifth S.L. Eye relatively deep with large, rounded lobe of pigment over lens in smaller larvae.

FINS: In the smallest positively identified specimen (14.8) only the caudal and anterior anal rays are ossified but 26 or more anal radials are present. Pelvic fins appear as buds in ventrolateral abdominal cavity wall at or below level of intestine behind a vertical through dorsal base. Dorsal adipose fin extends slightly in advance of a vertical through anal origin in smallest identifiable larvae (14.8-15.0) but is restricted to adult size in specimens 22-24 mm. and larger. Ventral adipose never larger than one-third pelvic-anal distance, reabsorbed in specimens 27-30 mm. and larger. All fin rays ossified in specimens 23-25 mm. and larger. Order of fin ray ossification: caudal, anal, dorsal, dorsal pectoral, pelvic, ventral pectoral. Pelvics in larger specimens inserted beneath or behind last dorsal ray.

PERITONEAL SECTIONS: Three peritoneal sections. All three sections developed in 14.8 mm. larva. One anterior section, dorsomedial to gut, and two posterior, paired sections, centered longitudinally over anus. Anterior section appearing well behind pectoral base, nearly to vertical through dorsal origin in some specimens. In a number of larvae, 15.0-19.0 mm. in size, only the posterior sections are present, and in no specimen is only the anterior section present, indicating that in *S. guentheri*, unlike *S. analis*, the posterior sections are formed first. However, in most larvae all three sections are present. Peritoneal sections expanding anteriorly, posteriorly, dorsolaterally, and ventrolaterally with growth, forming a complete tube around gut in adults. Anterior and posterior sections fuse over pelvic base in 45-55 mm. in size.

DERMAL PIGMENTATION: Dermal pigmentation appears as a pigment spot or spots on midlateral caudal peduncle just in advance of bases of midcaudal rays. Pigmentation first appears in specimens 15-17 mm. in size and is present in all specimens 17 mm. and larger. Area with pigmentation expands uniformly to cover caudal peduncle with large, more or less evenly scattered melanophores in specimens 25-28 mm. in size, but in specimens this size and smaller no pigment occurs ahead of a vertical through last anal ray (fig. 54C). Pigmentation of head, particularly on snout, appearing in specimens 35-40 mm. and larger.

GUT: Post-pelvic gut length in material I have examined (14.8 mm. and larger) is never less than two-thirds pelvic-anal distance. Anus at adult position, just anterior to anal origin, in specimens 27-30 mm. and larger. Expansion of caecum first evident in specimens 28-35 mm. Caecum extending in posterior direction, reaching nearly to pelvic insertion in specimens 40-45 mm.

METAMORPHOSIS: Completion of metamorphosis defined as point of fusion of anterior and posterior peritoneal sections over pelvic base concomitant with maximum rearward expansion of caecum, to just before anus in adult specimens. This point occurs in *S. guentheri* in specimens 50-55 mm. in size and 50 mm. is rather arbitrarily taken as the dividing line between metamorphic and larval specimens and adults.

Discussion.—Despite the extremely broad range of this species, there seems to be little geographic variation. Body proportions remain remarkably constant despite the wide range of habitats represented. Pigmentation, shape of the lateral line scales, and larval characteristics do not differ noticeably. The following meristic differences appear to me to be

Lateral line scales	47	48	49	50	51	52	N
Subtropical Convergence and							
Eastern South Pacific	_	_	2	4	15	1	22
All other localities	6	12	18	14	_	—	50
Vertebrae	46	47	48	49	50	51	N
Subtropical Convergence and							
Eastern South Pacific	—	—	—	1	8	2	11
All other localities	2	2	2	7	1	_	14
Pectoral fin rays	18	19	20	21			N
Eastern North Pacific	_	1	4	2			7
Equatorial Pacific	2	6	1				9
Subtropical Convergence and							
Eastern South Pacific	14	14	4	_			32
All other localities	18	41	_	_			59

TABLE 8. Meristic variation in Scopelarchus guentheri.

the most significant differences I have found between different populations of this species.

Specimens from the Subtropical Convergence and Transition Region of the South Pacific have more lateral line scales and vertebrae than specimens from warmer waters (table 8). In view of the well-known inverse correlation between water temperature during development and the number of meristic elements formed (e.g., Hubbs, 1922; Barlow, 1961; Johnson and Barnett, in press), this difference is not surprising.

All specimens of *S. guentheri* from the Atlantic Ocean have seven dorsal rays (15/15 counted) whereas in material of this species from the rest of the world this count ranged from 7-8 (23/85 or 27 per cent have dorsal = 7; 62/85 or 73 per cent have dorsal = 8). There are no other apparent differences between specimens from the Atlantic Ocean and specimens from elsewhere, and the biological significance of this difference is unclear to me.

Finally, of 107 specimens of S. guentheri counted, the range for 96 specimens from all oceans was 18-19 pectoral rays, but 11 had 20-21 pectoral rays. The peculiarity is that all 11 specimens were either from Transition waters of the eastern North Pacific, off southern California and Baja California (Catalina Basin to near Cedros Island, Mexico, and west to ca. 121° W); eastern equatorial Pacific (one specimen, pectoral = 20/20, 01° 57.5' N, 110° 39.0' W), or from the transition region of the eastern South Pacific and the Subtropical Convergence of the South Pacific. The usual range of pectoral counts in scopelarchids is 4-5, thus the range exhibited by S. guentheri, 18-21 rays, is not unusual. However, it does seem significant that all specimens of this species possessing more than 19 pectoral rays were from a relatively limited portion of the range of the species. The meaning of the difference, in the absence of other recognizable differences between specimens with elevated pectoral counts and those without, can only be explored after additional specimens of S. guentheri are obtained from the eastern Pacific, particularly from off California

Distribution.—Scopelarchus guentheri is a circumglobal warm-water species found in all three oceans, from the equatorial North Atlantic to the eastern Pacific. S. guentheri is the only scopelarchid known to occur in the Indian Ocean north of 5-10° N. This species appears to be more abundant around the peripheries of the central gyrals in the Pacific (fig. 55) than in the central portions of the central gyrals.

In warm-water areas larvae of *S. guentheri* have been taken throughout the year. In the transition region and Subtropical Convergence of the South Pacific larvae have been taken only in October - March (17 specimens, 12 collections), and most commonly in December and January (11





specimens, seven collections). Adults have been taken in this area in January (one specimen), February (one specimen), July (five specimens, three collections), and August (14 specimens, eight collections). But obviously more sampling needs to be done in order to say that larvae of *S. guentheri* are present in this area only during the southern summer.

Larvae have been captured in numerous hauls between the surface and 100-150 m. at night. Adults have been captured in the upper 150 m. at night, and in the upper 300 m. at day (one specimen), but very few daytime hauls, based on my material, have taken this species.

Material examined.—A total of 205 (7.0-119.0) specimens, including 18 (7.0-17.1) tentatively identified as *S. guentheri*, from 121 collections. **North Atlantic. DANA:** D1161 111, 1 (63.0). D1163 111, 1 (62.5). D1168 1V, 4 (38.0-62.5). D1171 1V, 1 (49.5). D1177 11, 1 (53.0). D1178 11, 1 (54.5). D1214 111, 1 (27.0).

South Atlantic. DANA: D3981 111, 1 (43.6). D3996 V11, 2 (47.4-54.5). D3997 1, 1 (85.3). ISH: ISH 1633, 1 (91.0). ISH 1740, 1 (67.5). ISH 1843, 1 (78.5).

Indian Ocean. DANA: D3804 111, 1 (18.0) + ? 6 (7.0-17.1). D3812 111, 8 (17.0-28.1). D3817 111, 1 (40.5). D3821 11, 1 (21.1). D3821 111, 2 (28.0-42.5). D3828 V, 1 (84.1). D3828 X, 1 (85.2). D3828 X1, 1 (68.2). D3828 X111, 1 (88.5). D3828 XV, 1 (70.5). D3847 1V, 1 (28.5) + ? 4 (9.4-12.5). D3849 1, 2 (19.9-21.5). D3904 1, 1 (96.0). D3904 111, 4 (33.0-55.5). D3908 11, 9 (19.1-45.1) + ? 4 (8.5-15.5). D3910 1, 3 (41.6-64.6). D3915 11, ? 3 (12.0-12.5). D3916 111, 1 (26.4). D3921 111, 1 (26.1). D3922 1, 2 (33.0-47.5). D3922 11, 1 (31.0). D3929 1, 1 (23.5) + ? 1 (15.0). D3941 1, 1 (26.5). D3966 11, 1 (32.1). D3969 111, 1 (26.0). D3969 1V, 1 (23.1). S10: S1069-21, 1 (112.4). S1069-23, 2 (18.1-28.0). SOSC: AB 1-17, 1 (73.0). AB 5-287B, 7 (21.8-25.0). TV 5-186, 1 (17.5). USNM: AB 3-8, 1 (106.5). AB 3-9, 1 (83.1). AB 6-333A, 1 (57.5). AB 6-341B, 1 (22.5). AB 6-344A, 1 (21.5).

Western Pacific. DANA: D3680 V1, 1 (94.5). S10: S1061-30, 1 (39.0). S1061-542, 1 (27.1). S1061-543, 1 (41.9). S1061-588, 4 (17.0-18.5). S1061-637, 2 (15.8-23.2). S1061-638, 1 (26.9). S1061-650, 1 (83.5). S1069-19, 7 [6 (15.0-25.5) + 1 (98.5)]. S1070-341, 1 (41.1). USNM: USNM 135417, 1 (93.6).

Equatorial Pacific. NMFS: HMS 31-73, 2 (23.5-24.0). HMS 31-121, 1 (31.5). HMS 33-18, 2 (21.0-23.1). **ORSTOM:** 24/9/68, 1 (58.0). No data, 1 (94.5), probably from vicinity 00° N, 170° E. BORA 11-11A, 1 (96.6). BORA 11-13A, 1 (119.0). CYCLONE V-1, 1 (97.0). **SIO:** S1052-83, 1 (32.6). S1055-265, 1 (26.0). S1056-109, 1 (93.0). S1060-144, (13.5).

Central South Pacific. S1O: S1O69-342, 1 (23.6). S1O70-113, 1 (43.4). S1O70-118, 1 (30.5).

South Pacific, Subtropical Convergence and Transition Region of Eastern South Pacific. S10: S1058-246, 2 (29.9-30.6). S1063-1008, 1 (26.0). S1063-1009, 2 (23.1-25.5). S1065-622, 1 (39.6). S1065-631, 1 (42.5). S1069-320, 1 (26.0). S1069-321, 1 (22.5). USC: USC-E (numbers are *Elianin* Station Numbers): 1723, 3 (59.6-63.2). 1731, 2 (58.7-64.0). 1739, 1 (58.5). 1761, (64.5). 1764, 2 (69.0-72.6). 1774, 2 (64.5-67.1). 1776, 1 (60.3). 1786, 1 (70.2). 1792, 1 (64.0). 1793, 3 (59.7-64.1). 1794, 3 (60.3-65.9). USNM: USNM 201153, 1 (93.8). WHOI: (numbers given are station numbers from *Anton Braun* cruise X111); 7, 1 (42.5). 10, 1 (50.0). 16, 1 (29.6). 20, 1 (28.5). 23, 1 (30.6). 43, 5 (39.1-74.5). 46, 1 (34.5).

Central North Pacific. NMFS: HMS 30-15, 3 (22.0-28.6). No data, probably Central North Pacific, 1 (32.2). JRM 21-2, 1 (34.5). **SIO**: S1O60-252, 1 (90.3). S1O68-492, 1 (18.0). S1O68-507, 1 (20.9). S1O68-537, 1 (43.6). S1O69-355, 1 (28.1). S1O: uncat. Climax 11, Aug. 18, 1969, 3 (20.5-28.1). UH: 70 (7/21, 1 (26.1). 70/9/11, 1 (48.5). 70/9/17, 1 (102.5).

Eastern North Pacific. LACM: LACM 9027, 1 (29.5). LACM 9077, 1 (30.5). LACM 9086, 1 (23.1). LACM 9694, 1 (88.4). SIO: SIO54-96, 1 (42.0). SIO63-445, 1 (59.5). SIO64-16, 1 (50.9). SIO64-39, 2 (20.0-29.0). SIO69-486, 1 (26.0).



FIG. 56. Scopelarchus michaelsarsi Koefoed 1955. A. Young adult, Field Museum of Natural History 49851, 30.8 (after Rofen, 1966e, p. 596). B. Lateral line scale above anal origin. UH 70 9 5, 54.5. C-E. Scales, ORSTOM CYCLONE V-2, 81.5. C. Lateral line scale above pectoral insertion. D. Penultimate lateral line scale. E. Body scale from immediately above lateral line. F. Ultimate lateral line scale, ORSTOM CYCLONE III-1, 91.0.

Scopelarchus michaelsarsi Koefoed 1955. Figure 56.

Scopelarchus analis (Brauer) in part: Beebe, 1937, p. 205. Grey, 1955, p. 284 (both according to Rofen, 1966e, p. 601).

Scopelarchus michaelsarsi Koefoed, 1955, pp. 6-7.

Scopelarchus cavei Marshall, 1955, pp. 307-308.

Phanops michaelsarsi Rofen, 1963, p. 4; 1966e, pp. 595-601.

Phanops cavei Rofen, 1963, p. 4; 1966e, p. 595.

Holotype.—28.5 mm. S.L. Michael Sars Expedition, Sta. 67, North Atlantic 40° 17' N, 50° 39' W, June 27, 1910.

Comparative diagnosis.—A species of Scopelarchus with 7-9 dorsal rays, 18-21 anal rays, 18-21 pectoral rays, and 40-44 lateral line scales; medial face of pectoral fin covered with dense black pigment over entire fin except five ventralmost rays. S. michaelsarsi is distinguished from S. analis (Brauer) and S. guentheri Alcock in the diagnoses of those species. S. michaelsarsi and S. stephensi cannot be distinguished on the bases of meristic characters (tables 1-5) but adults of *S. michaelsarsi* may be distinguished from adults of *S. stephensi* by the following characters: pigment on pectoral fin jet-black, covering entire fin except five ventralmost rays cf. pigment on pectoral fin a limited patch of melanophores situated between second and sixth or seventh (counting from dorsal) pectoral rays on medial one-third of fin, present neither at fin ray bases nor on distal third of fin; appressed pectoral fin reaching to or beyond anal origin, cf. appressed pectoral fin reaching pelvic insertion but not anus; least depth of caudal peduncle 8.8-10.8 per cent S.L., cf. 7.9-9.2 per cent S.L.; lateral line scale above anal origin: H/L 1.22-1.56, cf. 1.68-2.11; T/L .458-.605, cf. .602-.810; P/L .184-.279, cf. .260-.345.

Description.—Based on 50 (12.0-34.9) larvae and metamorphosing specimens and 19 (35.5-101.5) adolescents and adults. With the exception of meristic characters, the description given first is that of adults, followed by an account of development.

MERISTIC CHARACTERS: Values in parentheses are those of the holotype (taken from Koefoed, 1955, pp. 6-7). Dorsal 7-9 (7), 23/26 had dorsal = 8; anal 18-21 (18); pectoral 18-21 (21); lateral line scales 40-44 (ca. 45); vertebrae 40-44.

PROPORTIONAL DIMENSIONS: Based on 16 (33.4-96.8) specimens: North Atlantic Ocean: DANA 1242 I, 1 (45.0); ISH 525, 1 (61.3); ISH 783, 1 (96.8); USNM ACRE 7-14, 1 (33.4); WHOI RHB 1295, 1 (43.6); South Atlantic Ocean: ISH 1087, 2 (50.0-51.4); ISH 1259, 1 (37.6); Western Pacific Ocean: DANA 3714 I, 1 (67.5); DANA 3740 I, 1 (64.0); Western Equatorial Pacific: ORSTOM, Cyclone III-1, 1 (91.0); Cyclone 111-3, 1 (53.3); Cyclone IV-9, 1 (55.1); Cyclone V-2, 1 (81.5); North Central Pacific: UH 70/9/5, 1 (54.5); UH 70/9/9, 1 (68.0). Expressed as thousandths of the standard length and given as the mean, range (in brackets), and values for the holotype (in parentheses): Body, depth at dorsal origin, 210 [190-241] (211). Caudal peduncle: least depth, 95 [88-108] (105); length, 146 [132-163]. Adipose fin: distance to midcaudal rays, 192 [165-213]; length of base, 37 [29-45]; length of fin, 59 [50-67]. Anal fin: length of base, 246 [220-269]; length of longest ray, 100 [80-130]. Dorsal fin: length of base, 58 [46-68]; length of longest ray, 116 [80-156]; dorsal origin to anal origin (distance between verticals), 235 [195-295]; end of dorsal base to base of midcaudal ravs, 543 [515-580]. Pectoral fin, length of longest ray, 234 [176-295]. Pelvic fin, length of longest ray, 111 [83-160]. Pelvic insertion to anal origin, 161 [130-198]. Pectoral insertion to pelvic insertion, 229 [210-244]. Anus to anal origin, 42 [32-53]. Distance from snout to: anus, 604 [551-653]; dorsal origin, 423 [392-469]; (474); anal origin, 642 [595-697] (579); pectoral insertion, 291 [272-326]; pelvic insertion, 486 [455-528] (491); orbit, 70 [55-80] (88). Head length, 254 [232-273] (281). Postorbital head length, 109 [99-117]. Orbit: horizontal diameter, 78 [67-97] (70); vertical diameter, 76 [67-95] (77). Interorbital width, 35 [22-57] (39). Upper jaw length, 181 [160-198]. Lower jaw length, 195 [185-217] (211). Longest dentary tooth, 34 [28-43].

BODY: Body depth 4.78 [4.16-5.26] in S.L. Peduncle depth 2.69 [2.48-3.11] in H.L. Peduncle length 1.74 [1.51-1.94] in H.L.

SKIN AND SCALES: Body scales large; those scales adjacent to lateral line scales nearly as large as lateral line scales and overlapping all but posterior one-third of lateral line scales. About five series of scales from lateral line to dorsal origin and seven or eight series from lateral line to anal origin. About 24 series of body scales from occiput to dorsal origin and about 42 series from dorsal origin to adipose fin origin. Lateral line scales large, numbering 40-44 in 20 specimens counted. Lateral line scale above anal origin, based on 15 [Atlantic, 6 (31.3-96.8); Western Pacific, 2 (25.2-67.5); Equatorial Pacific, 5 (30.4-91.0); Central North Pacific, 2 (54.5-68.0)]: height/length 1.38 [1.22-1.56]; tympanum height/length, .523 [.458-.606]; pore height/length, .226 [.184-.279]; tympanum large, alate, smoothly indented at anterior margin, completely covering moderate central pore. Lateral line scale above pectoral insertion, based on 7 specimens [Atlantic, 1 (96.8); Equatorial Pacific, 4 (53.3-91.0); Central North Pacific, 2 (54.4-68.0)]: height/ length, 1.34 [1.20-1.50]; tympanum height/length, .546 [.482-.585]; pore height/length, .252 [.227-.285]; tympanum smoothly indented anteriorly. Penultimate lateral line scale, based on 3 [Equatorial Pacific, 2 (81.5-91.0); Central North Pacific, 1 (54.5)] and listed in that order: height/length, 1.45, 1.37, 1.34; tympanum height/length, .622, .574, .526; pore height/length, .290, .240, .310. Ultimate lateral line scale, based on one (91.0) Equatorial Pacific specimen: height/ length, 1.11; imperforate, circuli incomplete, no posterior field, reaching nearly to base of midcaudal rays.

HEAD: Eye diameter somewhat greater than snout length in adult specimens. Head length 3.95 [3.66-4.31] in S.L. Snout length 3.66 [3.30-4.22] in H.L. Horizontal eye diameter 3.28 [2.81-3.68] in H.L. Postorbital head length 2.33 [2.00-2.72] in H.L. Interorbital width 7.61 [4.69-10.60] in H.L. Pectoral insertion opposite indentation in gill cover at opercle-subopercle border.

Pseudobranchiae well-developed. Counts: (61.3) 14; (96.8) 18. Gill filaments extending to but not beyond margins of gill covers. Gill membranes united under anterior margin of eye.

MOUTH: Upper jaw length 1.41 [1.24-1.54] in H.L. Lower jaw length 1.31 [1.17-1.42] in H.L. Upper jaw extends well beyond vertical through posterior margin eye, nearly to anteroventral angle of preopercle.

Tooth counts based on 4 (45.0, 51.4, 61.3, 96.8) specimens and listed in that order. Premaxillary tooth counts: 38, 39, 42, 75. Dentary tooth counts: lateral, 21, 17, -, 22; medial, 9, 8, -, 8. Palatine tooth counts: 12, 12, 13, 16. Longest dentary tooth 7.65 [6.25-9.48] in H.L. Lingual tooth counts: 10, 7, 11, 12.

F1NS: Dorsal moderate: longest dorsal ray 11.6 [8.0-15.6] per cent S.L.; length of dorsal base, 5.8 [4.6-6.8] per cent S.L. Appressed pelvic fins reach to or slightly past anus but not to anal origin. Pelvic rays thinner and shorter than pectoral rays. Length of longest pelvic ray 11.1 [8.3-16.0] per cent S.L.; length of longest pectoral ray 23.4 [17.6-29.5] per cent S.L. Appressed pectoral fins reaching slightly beyond anal origin in best preserved specimens. Anal base short, 24.6 [22.0-26.9] per cent S.L.

COLOR: Dermal pigment on body limited to stripes dorsal and ventral to lateral line typical for species of *Scopelarchus*. Scale pockets edged with pigment dorsal but not ventral to lateral line. Caudal peduncle and scaly flaps of skin overlying bases of caudal rays well pigmented. Lateral line scale pockets edged with pigment. Three to four lines of pigment above and below midcaudal rays directed posteriad on membranes between rays of caudal fin, and extending nearly to tip of caudal fin. Pigment lacking on anal and adipose fins. Dorsal fin pigmented on base and entire area of fin except for last two rays. Extremely dense pigment on medial face of pectoral fin and fin base described in comparative diagnosis. Pigment lacking on pelvic fin in all specimens except [ISH 783, 1 (96.8)] where dense pigment is present on lateral portions of fin rays and membranes. Peritoneum dense black.

Development.—The description of development in S. michaelsarsi is based on 50 (12.0-34.9) larval and metamorphic specimens. Measurements, expressed as percent standard length, are given as the mean and range (values in brackets) and are based on 26 [Atlantic: DANA 1168 IV, 1 (32.0); DANA 1182 II, 1 (18.0); USNM ACRE 3-7, 1 (16.0); ACRE 3-13, 1 (14.5); ACRE 4-21c, 1 (26.1); ACRE 7-14, 1 (30.8); WHOI RHB 1292, 1 (22.5). Indian Ocean: DANA 3812 III, 1 (12.0); DANA 3849 I, 4 (14.1-18.4). Western Pacific: DANA 3791 II, 3 (17.5-20.5). Western Equatorial Pacific: ORSTOM BORA IV-11B, 1 (30.4); CYCLONE II-14, 2 (26.7 - 35.5); CYCLONE II-18, 1 (34.9). South Central Pacific: USNM: RHG E 31 - 25A, 2 (14.9-18.1). North Central Pacific: SIO69-355, 1 (17.4); SIO70-110, 1 (29.0); SIO70-111, 1 (22.1); UH 70/7/19, 1 (14.7); UH 70/7/30, 1 (17.9).] specimens. Figure 57 illustrates in sequence the development of this species.





RECOGNITION.—Larvae of S. michaelsarsi can be distinguished from larvae of other Scopelarchus species through the following combination of characters: dorsal 7-9; anal 18-21; pectoral 18-21. Larvae of S. michaelsarsi are extensively compared with each of the other three species of Scopelarchus: S. analis, S. guentheri, and S. stephensi in the respective larval recognition sections of those species.

BODY: Body short, deep, with deep peduncle, peduncle depth 9.4 [7.7-11.5]. Head usually exceeding one-fourth of standard length, head length 25.7 [23.6-29.6]. Eye relatively narrow and deep with deep choroid cone in smaller larvae, eye length/eye diameter (based on pigmented portions only) varies from 3.00-2.26 over size range examined (12.0-18.1).

FINS: In smallest available specimens [DANA 3812 III, 1 (12.0); SIO61-588, 1 (12.0)] the principal caudal, dorsal, and anal rays are ossified as are most pectoral rays. Pelvics present as buds in ventrolateral margin of body wall on level with ventral contour of gut and inserted beneath dorsal ray. Dorsal adipose extends anterior of vertical through anal origin. Ventral adipose occupies about one-third of pelvic-anal distance. All fin rays ossified by specimens 16-17 mm. in size. Dorsal adipose reduced to adult dimensions by specimens 20 mm. in size and ventral adipose absent from specimens larger than 20-22 mm. in size. Apparent order of fin ray ossification: caudal-dorsal-anal; dorsal pectoral; pelvic, ventral pectoral. In larger larvae pelvics usually inserted beneath or slightly behind vertical through last one or two dorsal rays.

PERITONEAL SECTIONS: Three peritoneal sections. All three sections present and well-developed in smallest available larvae. Peritoneal sections fuse over pelvic base and form complete tube in specimens larger than 32-35 mm. in size.

DERMAL PIGMENTATION: Dermal pigmentation in *S. michaelsarsi* similar to that of other *Scopelarchus* species. Dermal pigmentation on body apparently marked by appearance of patch of melanophores at midcaudal peduncle at and slightly forward of terminus of lateral line. Dermal pigmentation apparently spreads rapidly anteriad dorsal and ventral to the lateral line resulting in specimens15 mm. and larger having essentially adult dermal pigmentation patterns. Head, pectoral, and scale pocket pigmentation is present in larvae 18 mm. and larger resulting in larvae about 20-22 mm. and larger presenting typically adult pigmentation in all respects but that associated with the peritoneum.

GUT: In all material I have seen, the post-pelvic gut length is never less than two-thirds the pelvic-anal distance, and is this short only in the smallest larvae. Specimens 18 mm. and larger have essentially adult pelvic-anus proportions. Expansion of the caecum evident in 18-20 mm. specimens and reaches to near anus, as in adults, in 28-30 mm. specimens.

TABLE 9. Comparison of counts and measurements of S. michaelsarsi and S. cavei.

METAMORPHOSIS: If initiation of metamorphosis is defined as appearance of all peritoneal sections and coincident appearance of dermal pigmentation, all specimens I have examined of *Scopelarchus michaelsarsi* are metamorphic. Completion of metamorphosis occurs as early as 33.4 mm. (Acre 7-14N) and is complete in specimens 35 mm. and larger. Completion of metamorphosis is defined for this species as fusion of anterior and posterior peritoneal sections, which occurs in a line over the pelvic base, and dorsomedial and ventrolateral expansion of peritoneal sections to form a complete tube of pigment around the gut.

Discussion.-Comparison of Koefoed's (1955, pp. 6-7) description of Scopelarchus michaelsarsi with Marshall's (1955, pp. 307-308) description of Scopelarchus cavei led Rofen (1966e, p. 595) to recognize both species as valid and distinguished from one another by snout length ("snout length longer than horizontal eve diameter" in Scopelarchus michaelsarsi, cf. "snout length shorter than horizontal eye diameter," in S. cavei.) and by the insertion of the pelvic fins ("ventral fins inserted behind a vertical from base of dorsal fin" in S. cavei, cf. "ventrals inserted under anterior rays of base of dorsal fin" in S. michaelsarsi). Both Koefoed and Rofen had small specimens (table 9) whereas Marshall's single specimen of S. cavei was fairly large. In my material most specimens have the pelvics inserted under the last one or two dorsal rays or slightly behind a vertical through the last dorsal ray. All specimens having the pelvics inserted under the middle of the dorsal base are small (e.g., 25.5, 33.4, 45.0 Atlantic, 14.7, 17.9, 29.2 Pacific) and contrariwise all specimens 50 mm. and larger have the pelvics inserted under or slightly behind the last dorsal ray in all three oceans. The snout length is considerably greater than the horizontal eye diameter in all young scopelarchids. With regard to all other characters provided by Koefoed, Marshall, and Rofen, the agreement between Scopelarchus michaelsarsi and S. cavei is excellent, and I can find no basis in my material for recognizing two distinct species. As Koefoed's description of S. michaelsarsi (April, 1955) antedates Marshall's description of S. cavei (August, 1955), I regard S. cavei as a junior synonym of S. michaelsarsi.

Distribution.—Scopelarchus michaelsarsi is nearly circumglobal in warm-waters and is known from all three oceans (fig. 58). It is known from the western (but not the eastern) North Atlantic, from the central South Atlantic, throughout the Indian Ocean, the South China Sea, and the semiisolated seas of the Indo-Malayan Archipelago, and from the central North and South Pacific. S. michaelsarsi enters Pacific Equatorial water, but apparently only in the far west (170° E). S. michaelsarsi is apparently replaced by S. stephensi in the central North Pacific north of Hawaii (fig. 58).





Larvae have been taken throughout the year throughout the known range of this species. Larvae have been taken, at night, on a number of occasions in hauls shallower than 200 m., but have never been taken in hauls shallower than 100 m. Larvae have been taken in only three daytime hauls to less than 500 m. Adults have never been taken in hauls shallower than 256 m. at night, and most were taken in hauls to 500 m. or deeper. To my knowledge, adult *S. michaelsarsi* have been taken in only one daytime haul shallower than 500 m. (0-435 m).

Material examined.—A total of 69 (12.0-101.5) specimens from 53 collections. North Atlantic. DANA: D1168 IV, 1 (32.0); D1182 II, 1 (18.0); D1242 I, 1 (45.0). ISH: ISH 525, 1 (61.3); ISH 783, 1 (96.8); ISH 2389, 1 (62.7); ISH 2439, 1 (70.1). USNM: OCEAN ACRE, ACRE 3-7, 1 (16.0); ACRE 3-13, 1 (14.5); ACRE 3-14, 1 (14.9); ACRE 4-21c, 1 (26.1); ACRE 6-16b, 1 (15.0); ACRE 7-14, 2 (30.8-33.4); ACRE 9-2b, 1 (14.0); ACRE 9-9, 1 (16.4); ACRE 9-15, 1 (32.0); ACRE 9-19, 1 (19.5); ACRE 9-21, 1 (17.0); ACRE 10-26n, 1 (20.0); ACRE 11-13m, 1 (15.1). WHOI: RHB 1292, 1 (22.5); RHB 1295, 1 (43.6); RHB 1305, 2 (25.4-27.4).

South Atlantic. ISH: ISH 1087, 2 (50.0-51.4); ISH 1259, 1 (37.6); ISH 2035, 1 (101.5). Indian Ocean. DANA: D3812 111, 1 (12.0); D3849 1, 4 (14.1-18.4); D3941 I, 2 (13.0-20.5); D3969 111, 1 (12.8). SOSC: AB 6-336A, 1 (17.1).

Western Pacific. DANA: D3714 1, 1 (67.5); D3739 11, 1 (29.2); D3740 1, 1 (64.0); D3791 11, 4 (13.5-20.5). SIO: SIO61-588, 3 (12.0-22.1); SIO70-346, 2 (21.0-25.2).

Western Equatorial Pacific. ORSTOM: BORA IV-11B. 1 (30.4): CYCLONE 11-14. 2 (26.7-35.5); CYCLONE 11-18, 1 (34.9); CYCLONE 111-1, 1 (91.0); CYCLONE 111-3, 1 (53.3); CYCLONE IV-9, 1 (55.1); CYCLONE V-2, 1 (81.5).

Central South Pacific. SIO: S1070-110, 1 (29.0); S1070-111, 1 (22.1); S1070-118, 2 (14.1-17.0). **USNM:** E31-25A, RHG 67-72, 2 (14.9-18.1).

Central North Pacific. SIO: S1069-355, 1 (17.4). UH: UH 70/7/19, 1 (14.7); UH 70/7/ 30, 1 (17.9); UH 70/9/5, 1 (54.5); UH 70/9/9, 1 (68.0).

Scopelarchus stephensi Johnson 1974. Figure 59.

Scopelarchus stephensi Johnson 1974, pp. 455-456.

Holotype.—55.0 mm. S.L. SIO68-486. Central North Pacific, 27° 56.9′-28° 7.9′ N, 177° 53.4-39.2′ W (1KMT) September 21, 1968.

Comparative diagnosis.—A species of Scopelarchus with 8 dorsal rays, 20-22 anal rays, 18-20 pectoral rays, and 41-44 lateral line scales; pigment on pectoral fin limited to a patch of melanophores between second and sixth or seventh pectoral rays (counting from dorsal), and present on medial one-third of fin only, no pigment at bases of pectoral fin rays, and pigment not extending to distal one-third of fin. S. stephensi is distinguished from S. analis (Brauer), S. guentheri Alcock, and S. michael-sarsi Koefoed in the diagnoses of those species.

Description.—Based on 12 (14.8-25.8) larval and metamorphosing specimens and 14 (54.5-62.0) adults. With the exception of meristic characters, the description based upon adults is given first followed by



FiG. 59. Scopelarchus stephensi. A. Holotype, SIO68-486, 55.0. B. Lateral line scale above anal origin. SIO68-483, 60.5. C. Lateral line scale above pectoral insertion, SIO68-542, 58.6. D. Penultimate lateral line scale, NMFS HMS 30-63, 56.8. E. Ultimate lateral line scale, SIO68-483, 57.5.

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a description of development.

MERISTIC CHARACTERS: Values in parentheses are those for the holotype. Dorsal fin 8 (all). Anal fin 20-22 (21). Pectoral 18-20 (18). Lateral line scales 41-44 (44). Vertebrae 42-43 (43).

PROPORTIONAL DIMENSIONS: Based on 12 (55.0-62.0) specimens: NMFS: HMS 30-63, 1 (56.8); SIO: S1O51-175, 1 (56.0); S1O60-411, 1 (62.0); S1O68-483, 4 (57.5-60.9); S1O68-486, 3 (55.0-58.9); S1O68-490, 1 (58.0); S1O68-542, 1 (58.6). Expressed as thousandths of the standard length, and given as the mean, range (in brackets), and values for the holotype (in parentheses): Body, depth at dorsal origin, 194 [173-214] (173). Caudal peduncle: least depth, 85 [79-92] (84); length, 153 [144-162] (144). Adipose fin: distance to midcaudal rays, 189 [179-204] (184); length of base, 37 [27-46] (36); length of fin, 59 [49-79] (49). Anal fin: length of base, 254 [234-268] (245); length of longest ray, 107 [102-115] (102). Dorsal fin: length of base, 58 [51-70] (56); length of longest ray, 114 [105-124] (111); dorsal origin to anal origin (distance between verticals), 229 [215-263] (226); end of dorsal base to base of midcaudal rays, 550 [505-588] (553). Pectoral fin, length of longest ray, 179 [155-200] (200). Pelvic fin, length of longest ray, 100 [81-119] (102). Pelvic insertion to anal origin, 157 [136-194] (156). Pectoral insertion to pelvic insertion, 222 [205-235] (212). Anus to anal origin, 44 [32-52] (44). Distance from snout to: anus, 573 [547-591]; dorsal origin, 402 [382-422] (409); anal origin, 610 [586-622] (600); pectoral insertion, 268 [256-286] (262); pelvic insertion 454 [438-470] (444); orbit, 61 [56-64] (64). Head length, 241 [223-246] (245). Postorbital head length, 105 [98-110] (109). Orbit: horizontal diameter, 74 [68-80] (74); vertical diameter, 74 [69-78] (73). Interorbital width, 15 [32-38] (36). Upper jaw length, 168 [158-177] (174). Lower jaw length, 183 [165-191] (191). Longest dentary tooth, 29 [25-33] (27).

BODY: Body depth 5.20 [4.68-5.80] (5.80) in S.L. Peduncle depth 2.82 [2.56-3.09] (2.94) in H.L. Peduncle length, 1.57 [1.41-1.71] (1.71) in H.L.

SKIN AND SCALES: Body scales large; those scales adjacent to lateral line scales nearly as large as lateral line scales and completely overlapping all but posterior one-third of lateral line scales. About five series of scales from lateral line to dorsal origin, six or seven rows from lateral line to anal origin. About 24 rows from occiput to dorsal origin, and about 37 rows from dorsal origin to origin of adipose fin. Lateral line scales large, numbering 41-44 in 13 specimens counted. Lateral line scale above anal origin, based on 14 (54.5-62.0) specimens: height/length, 1.86 [1.68-2.11] (1.91); tympanum height/length, .713 [.602-.810] (.650); pore height/length, .302 [.260-.345] (.260); height of scale

considerably greater than length; tympanum large, alate, smoothly indented at anterior margin, completely covering large central pore. Lateral line scale above pectoral insertion, based on 10 (54.5-62.0) specimens: height/length, 1.58 [1.30-1.88]; tympanum height/length, .623 [.523-.677]; pore height/length, .282 [.216-.351]; tympanum irregularly shaped but usually indented anteriorly. Penultimate lateral line scale, based on seven (54.5-58.6) specimens: height/length, 1.70 [1.60-1.82]; tympanum height/length, .820 [.675-1.00]; pore height/length, .427 [.358-.500]. Ultimate lateral line scale, based on 4 (54.5, 55.5, 57.5, 58.0) specimens and listed in that order: height/length, .900, .895, 1.02, 1.20; imperforate, circuli incomplete, partially enclosing large central focus, not forming a posterior field, reaching nearly to base of midcaudal rays.

HEAD: Eye diameter noticeably greater than snout length. Head length 4.18 [4.06-4.48] (4.07) in S.L. Snout length 3.93 [3.75-4.15] (3.86) in H.L. Horizontal eye diameter 3.21 [2.92-3.39] (3.29) in H.L. Postorbital head length 2.28 [2.20-2.38] (2.25) in H.L. Interorbital width 6.87 [6.36-7.20] (6.75) in H.L.

Pseudobranchiae well-developed. Counts: (55.0, type) 12; (58.6) 12; (58.9) 11. Gill filaments moderate, not extending beyond margins of gill covers. Gill membranes united under anterior margin of eye.

MOUTH: Upper jaw length, 1.43 [1.35-1.47] (1.41) in H.L. Lower jaw length, 1.31 [1.25-1.42] (1.28) in H.L. Upper jaw extends slightly behind vertical through posterior margin of eye.

Tooth counts are based on 3 [55.0, type; 58.6, 58.9] specimens and listed in that order. Premaxillary tooth counts: 68, 64, 70. Dentary tooth counts: lateral, 27, 24, 27; medial, 11, 11, 12. Longest dentary tooth, 8.39 [6.75-9.50] (9.00) in H.L. Palatine tooth counts: 18, 11, 16. Lingual tooth counts: 12, 10, 12.

FINS: Dorsal moderate: longest dorsal ray 11.4 [10.5-12.4] per cent S.L.; length of dorsal base, 5.8 [5.1-7.0] per cent S.L. Appressed pelvic fins barely reach anus in specimens with best preserved pelvic fins. Pelvic rays thinner and shorter than pectoral rays. Length of longest pelvic ray, 10 [8.1-11.9] per cent S.L.; length of longest pectoral ray, 17.9 [15.5-20.0] per cent S.L. Appressed pectoral fins reaching slightly beyond pelvic fin insertion in best preserved specimens. Anal base short, 25.4 [23.4-26.8] per cent S.L.

COLOR: Pigment on body limited to dermal stripes dorsal and ventral to lateral line typical for species of *Scopelarchus*, pigment outlining scale pockets dorsal but not ventral to lateral line, and pigment on caudal peduncle at bases of caudal rays. Limited pigment on caudal fin above and below mid-caudal rays and extending one-fourth to one-third of caudal fin length along fin from bases of caudal rays. Pigment lacking on anal, pelvic, and adipose fins, and absent from bases of ventral procurrent rays. Pigment on pectoral described in comparative diagnosis. Peritoneum dense black.

Development.—The description of development in S. stephensi is based on 12 (14.8-25.8) larval and metamorphosing specimens. Measurements expressed as percent standard length are given as the mean and range (values in brackets) and are based on 12 (14.8-25.8) specimens: DANA 4774, 8 (14.8-22.5); DANA 4781, 1 (21.9); OSU 561-562, 1 (25.8); SIO63-423, 2 (19.1-19.5). Figure 57 illustrates in sequence the development of this species.

RECOGNITION: Larvae of S. stephensi can be distinguished from larvae of other Scopelarchus species through the following combination of characters: dorsal 8, anal 20-22, pectoral 18-20; pigment present on pectoral fin; peritoneal sections and dermal pigment as described for genus. Larvae of S. stephensi can easily be distinguished from those of S. guentheri (over the size range examined, 14.8-25.8) in having 22 or fewer anal rays, cf. 24 or more. Larvae of S. stephensi and S. michaelsarsi are extensively compared to those of S. analis in the larval recognition section of that species. As the larvae of S. stephensi and S. michaelsarsi closely resemble the adults (except for peritoneal pigment) after they reach a size of 22-25 mm. in S. stephensi and 20-22 mm. in S. michaelsarsi. specimens larger than this can be distinguished from each other by the characters given in the respective comparative diagnosis of each species. Although I have only seen 12 (14.8-25.8) larvae of S. stephensi, the following characters apparently separate the two species: dermal pigment stripes not appearing in S. stephensi in specimens smaller than 17.9 mm., not extending to over anal origin in specimens less than 20-22 mm. in size cf. dermal pigment stripes present and extending to or beyond anal origin (from caudal peduncle) in specimens of S. michaelsarsi larger than 15 mm.; [measurements based on 50 (12.0-34.9) S. michaelsarsi and 12 (14.8-25.8) S. stephensil, least peduncle depth 7.5 (5.4-8.7) per cent S.L., cf. 9.4 (7.7-11.5) per cent S.L.; Head length 21.8 (18.3-23.2) per cent S.L., cf. 25.7 (23.6-29.6) per cent S.L.

BODY: Body short, deep, with moderately deep peduncle, peduncle depth 7.5 [5.4-8.7] per cent S.L. Head nearly one-fourth of standard length, head length 21.8 [18.3-23.2] per cent S.L. Eye narrow and deep, with deep choroid cone in smaller larvae, eye length/eye diameter (based on pigmented portions only) varies from 2.92-1.30 over size range examined (14.8-25.8).

FINS: In smallest available specimen [DANA 4774, 1 (14.8)] principal caudal and dorsal rays are ossified, dorsal pectoral and anal rays are

beginning to differentiate. Pelvics present as small buds in ventrolateral margin of body wall on level with ventral contour of gut and inserted beneath last dorsal ray. Dorsal adipose extending to over anal origin. Ventral adipose occupies two-thirds of pelvic-anal distance. In next largest specimen [DANA 4774, 1 (16.1)] caudal, dorsal, anal, and dorsal pectoral rays completely differentiated, procurrent caudal rays beginning to form, pelvics in undifferentiated bud stage. Dorsal adipose extending to over anterior one-third of anal. Ventral adipose reduced to one-fourth of pelvic-anal distance. All fins are completely ossified in specimens 20 mm. and larger. Apparent order of fin ray ossification: caudal, dorsal, anal, dorsal pectoral, pelvic, ventral pectoral. Dorsal adipose reduced to adult dimensions in larvae 20 mm. and larger. Ventral adipose absent in a 25.8 mm. larva. In larger larvae pelvic insertion under or slightly behind last dorsal ray.

PERITONEAL SECTIONS: Three peritoneal sections. All three sections present in smallest available larva [DANA 4774, 1 (14.8)] but paired posterior sections in this specimen evident as mere dots of pigment about midway between pelvic insertion and anus. Anterior peritoneal section a dorsomedial transverse sheet, above gut and between pectoral bases. Paired posterior sections appear in dorsolateral abdominal cavity and remain entirely postpelvic and preanus in all but largest [DANA 4774, 2 (22.0-22.5); OSU 561-562, 1 (25.8)] specimens where they extend slightly posterior to anus. Anterior peritoneal section apparently expands rearward with rearward expansion of caecum, but remains separate from posterior sections and anterior to pelvic insertion in largest metamorphic specimen. Position of fusion between anterior and posterior sections unknown, but presumably occurs slightly in advance of pelvic insertion.

DERMAL PIGMENTATION: Dermal pigmentation in *S. stephensi* is similar to that of other *Scopelarchus* species. Appearance of dermal pigmentation marked by dots of pigment hypaxially on caudal peduncle in smallest larvae. Pigmentation expands forward from peduncle as stripes slightly above and below lateral line, with ventral stripe expanding slightly faster than dorsal stripe.

Head pigmentation first appears in 16.0 mm. larvae as dots of pigment at dorsoposterior corner of mandible. Cranial pigment appears by 20 mm. larvae, and head pigmentation essentially similar to that of adults in 22 mm. and larger specimens.

Pectoral pigment first appears in a 21.9 mm. larva in my material, and appears as dark pigment on and between six dorsalmost rays and on medial one-third of pectoral length. In the 25.8 mm. specimen pectoral pigmentation is present over the dorsal and distal two-thirds of the pectoral fin, and is presumably reduced to adult proportions during later growth.

GUT: 'Post-pelvic gut length one-third pelvic-anal distance in a 14.8 mm. larva, two-thirds pelvic-anal distance in 16.0 mm. larvae, and reaches adult proportions in 19-20 mm. larvae. Caecum nearly to pelvic insertion in largest (25.8) specimen.

METAMORPHOSIS: The initiation of metamorphosis in Scopelarchus and Scopelarchoides larvae is taken as the appearance of the paired peritoneal sections and dermal pigmentation. Therefore, by this definition, all of my material of Scopelarchus stephensi young stages are metamorphic specimens. The 25.8 mm. specimen is essentially adult in proportions, pigmentation, and presence of pigmented scale pockets and lateral line scales (evident only as scale pockets). Transitional metamorphic stages to smallest adult (55.0 mm.) are unknown but three additional changes are required to complete metamorphosis: fusion of peritoneal sections, expansion of peritoneal pigment to form tube around gut, rearward expansion of caecum to adult position just before anus. These changes, as well as appearance of gonad, etc., presumably occur between 25-33 mm. in size (cf. S. michaelsarsi, S. analis) and certainly occur between 25-55 mm. in size.

Distribution.—Scopelarchus stephensi is known only from the North Pacific. It is known from 26 [12 (14.8-25.8) + 14 (54.5-62.0)] specimens from 12 collections all between 25° 37.9-50.0' to 34° 23.0-50.0' N, 178° 07.3-31.9' E to 126° 37.5' W. Thus the distribution of S. stephensi as presently known forms a band roughly 8° of latitude deep stretching across the northern portions of both Western and Eastern North Pacific Central Water. Although S. analis has been taken throughout the range of S. stephensi, S. michaelsarsi has not been taken north of the nearshore waters of the Hawaiian Islands. Thus, apparently S. stephensi replaces S. michaelsarsi in the Central North Pacific. S. michaelsarsi is otherwise a nearly circumglobal warmwater species. The distribution of S. stephensi is illustrated in Figure 58.

Larvae of *S. stephensi* are known from four hauls made in March, April, and July. Larvae have been taken at night in the upper 100 m. (1, 21.9 mm., 183 mwo, DANA 4781). One adult was taken at night in a haul 0-210 m., all other hauls were to depths in excess of 1000 m. One adult specimen came from the stomach of an *Alepisaurus ferox* taken by a long-liner.

Material examined.—A total of 26 (14.8-62.0) specimens from 12 collections. DANA: 4774, 8 (14.8-22.5); 4781, 1 (21.1). NMFS: HMS 30-63, 1 (56.8); JRM 22-5, 2 (54.5-55.5); OSU: 561-562, 1 (25.8). SIO: 51-375, 1 (56.0); 60-411, 1 (62.0); 63-423, 2 (19.1-19.5); 68-483, 4 (57.5-60.9); 68-486, 3 (55.0-58.9); 68-490, 1 (58.0); 68-542, 1 (58.6).

EVOLUTIONARY RELATIONSHIPS OF THE SCOPELARCHIDAE

Both Marshall (1955) and Rofen (1966e) recognized a fundamental dichotomy in the array of scopelarchid species known to them: longbodied scopelarchids with the pelvic insertion in advance of the dorsal origin (Benthalbella) and short-bodied species with the pelvic insertion behind the dorsal origin (Scopelarchus, Scopelarchoides). Both authors lacked the critical material to expand their studies of relationships between scopelarchid species. Eight species, or nearly half the number in the family, have been recognized since Rofen's (1966e) paper: six species and the genus Rosenblattichthys as a result of the present work (Johnson, 1972. 1974). This new information has required a reinterpretation of the relationships between scopelarchid species and has made the previous arrangements of genera (Marshall 1955, Rofen, 1966e) untenable. especially on the basis of characters used by the earlier authors. The purpose of the present section is twofold: (1) to discuss characters and character states indicative of relationships between scopelarchid species; (2) to use this information to group scopelarchid species into biologically meaningful genera.

The interpretation of phylogenetic relationship is dependent upon the discovery of derived character states shared in common between two groups, and whose presence is due to immediate common ancestory (Brundin, 1966; Hennig, 1966). The difficulty arises in determining probable phyletic or directional sequence, i.e., primativeness or derivativeness, of the array of states exhibited by any given character. To determine the probable directional sequence of states of characters within the Scopelarchidae requires a detailed analysis of these characters in an adequate "outgroup," i.e., an adequate sample of non-scopelarchid (and especially other myctophiform) fishes. A detailed study of the osteology and larval morphology of other myctophiform (not to mention salmoniform, etc.) fishes is beyond the scope of this study. I intend to expand the analysis begun here to other myctophiform families and report the impact of this study on the classification of scopelarchids and evermannellids at a later date. Therefore, the present study is preliminary and the phylogenetic analyses are in a large sense a posteriori in that the genera of scopelarchids were erected on the basis of character states common to their included species (without regard to a detailed analysis of presumed directional sequence). Directional sequence was later predicted for those characters for which I felt I had adequate information [in determining "derivativeness" I follow the criteria established by Marx and Rabb (1970, 1972)]. There remain a large number of characters for which directional sequence has not been predicted, some of these are indicated in the discussion to follow.

Paralepidids have often been cited as the stem alepisauroid group while it has been suggested that among myctophoid myctophiforms that the chlorophthalmids are closer to the ancestor of the alepisauroids than any other extant myctophoid group. Most of the characters listed to document these statements constitute little more than a listing of those character states probably primitive for the entire chlorophthalmid-alepisauroid group. The list of characters compiled below is presented for two reasons: (1) to provide a preliminary view of the probable position of the Scopelarchidae among this group of fishes; (2) as a basis for preliminary determination of probable sequence of some scopelarchid characters. Some characters are sufficiently well understood to allow a discussion of probable primitiveness or derivativeness (within the array of scopelarchid species). States believed to be primitive are all identified with a "O," states believed to be derived are designated by positive integers. These characters are summarized in Table 10 and were the sole basis for the construction of Figure 60. Osteological statements for any given family are based solely on material listed as cleared and stained material in the osteological section above (except where characters could be determined externally or where reference is made to the literature).

1. PARIETAL BONES

Parietal bones are present and meet broadly in midline in Aulopus, chlorophthalmids (Rosen, 1971), and paralepidids (Parr, 1929). In most scopelarchids and in Omosudis (Parr, 1929) the parietals are reduced in size and widely separated by the supraoccipital. In six scopelarchid species (table 10) the parietals are absent, and presumably are fused with the expanded frontal bones. The loss of parietal bones is undoubtedly a derived feature. Two states of character 1 are recognized in scopelarchids:

(0) = parietals present

(1) = parietals absent

2. SUPPORT OF FIRST EPIBRANCHIAL

The support of the first epibranchial dorsally is through a suspensory or first pharyngobranchial, and short to elongate arms at about midlength on the first epibranchial and the second pharyngobranchial are connected by a ligament in most myctophiform fishes: *Aulopus*, myctophids (Paxton, 1972), chlorophthalmids, paralepidids, most scopelarchids (figs. 10, 11). The suspensory pharyngobranchial is lost and the first epibranchial is connected by a ligament to the anterior end of the third



FIG. 60. Representation of proposed relationships among species and genera of scopelarchids. Integers indicated on lines represent derived character states (see text).

pharyngobranchial in four alepisauroid families: Evermannellidae, Omosudidae, Alepisauridae, Anotopteridae. A striking shift in the support of the first epibranchial takes place in six scopelarchid species (table 10, fig. 11). As states (2, 3) represent ideal morphological intermediates between state (0) and state (4), four states of character 2 are

recognized in scopelarchids:

- (0) = suspensory pharyngobranchial present, hooklike arms on first epibranchial and second pharyngobranchial connected by a ligament.
- (2) = suspensory pharyngobranchial absent, support of first epibranchial near proximal end of second pharyngobranchial; hooklike arms on first epibranchial and second pharyngobranchial connected by a ligament.
- (3) = suspensory pharyngobranchial absent, support of first epibranchial at middle of second pharyngobranchial; no hooklike arms.
- (4) = suspensory pharyngobranchial absent, support of first epibranchial at point of articulation between second pharyngobranchial and second epibranchial; no hooklike arms.

3. BASIHYAL

Scopelarchids are apparently set apart from most myctophiform fishes in having a large, well-ossified basihyal with striking development of dentition on the associated tooth plate. The basihval is largely cartilaginous and ossified only proximally but with a well-ossified dentigerous dermal plate in Aulopus, chlorophthalmids, and paralepidids. The basihval is unossified in most (or all?) myctophids (Paxton, 1972). In evermannellids both dermal and endochondral elements are ossified but both are reduced to short splintlike (and edentate) structures suspended vertically between and just anterior to the anterior margin of the hypohyals. The remaining alepisauroids exhibit a much reduced basihval or this element is absent. The relative length of the basihval divides the scopelarchids into two groups (fig. 9) but as a short basihval is always associated with presence of basibranchial teeth whereas an elongate basihyal is always associated with absence of basibranchial teeth, and this is presumed to be functionally related, the variation in basihyal length in scopelarchids is included in character 4.

4. BASIBRANCHIAL TEETH

The presence of teeth over the basibranchials has been shown by Nelson (1969) to be widespread in primitive teleostean fishes and indicated by Nelson (1969, p. 497) to be the case in *Aulopus*. Teeth are present over the basibranchials in myctophids (Paxton, 1972), synodontids, and most scopelarchids. There are no basibranchial teeth in the chlorophthalmids or paralepidids I have examined, nor in other alepisauroids. Teeth occur over the basibranchials (fig. 9) in *Rosenblattichthys, Scopelarchus, Scopelarchoides danae*, and *S. nicholsi*. Lingual teeth are restricted to an elongate basihyal in *Scopelarchoides signifer*, *S. climax, S. kreffti*, and *Benthalbella*. The combined number and length of the lingual row of teeth whether restricted to the basihyal or present over the basibranchials as well, is about the same in both groups of scopelarchids. To regard the presence of basibranchial teeth as a de-

discussed in text. States considered primitive denoted by '0'; states considered derived denoted by positive integers. States presumed for inadequately known species indicated by "?." TABLE 10. Character states of 14 characters exhibited by scopelarchid species. Characters and character states defined and

Species	1	2	4	8	6	10	14	Chara 15	icters 16	17	18	19	20	21
Rosenblattichthys														
volucris	0	0	0	0	0	0	0	0	0	0	A18	A19	0	0
hubbsi	50	<u></u>	0	0	0	0	30	0;	30	0;	?A18	?A19	<u>5</u> 0	50
alatus	50	0;	0	0;	0	0	0	0	0	0	A18	A19	0	0
Scopelarchus														
stephensi	1:	?4	0	9	7	6	13	14	15	0	0	0	?A20	A21
michaelsarsi	1	4	0	9	7	6	13	14	15	0	0	0	A20	A21
analis	1	4	0	9	7	6	13	14	0	0	0	0	A20	A21
guentheri	1	4	0	9	7	00	13	14	0	0	0	0	A20	A21
Scopelarchoides														
danae	1	က	0	9	0	00	12	0	0	0	0	0	0	0
nicholsi	1	0	0	9	0	8	11	0	0	0	0	0	0	0
signifer	0	0	ŋ	9	0	0	0	0	0	0	0	0	0	0
climax	02	30	ŋ	56	0	0	0	0	0	0	0	0	50	0
kreffti	50	30	ŋ	9	0	0	<u>30</u>	<u>;0</u>	30	30	<u>50</u>	50	50	0
Benthalbella														
macropinna	0	0	ŋ	9	0	0	10	14	16	0	0	0	0	0
dentata	0	0	ŋ	9	7	00	10	14	16	17	0	0	0	0
infans	0	0	ŋ	9	2	00	10	14	16	17	0	0	0	0
linguidens	50	30	ß	36	7	8	10	14	16	17	0	0	50	0
elongata	0	0	ŋ	9	2	80	10	14	16	17	0	0	0	0

rived feature is consistent neither with Nelson's (1969) evidence nor with parsimony, since it might require postulation of an independent secondary acquisition of such teeth in both *Rosenblattichthys* and the *Scopelarchoides nicholsi - S. danae - Scopelarchus* groups (fig. 60). It is possible that the condition seen in the *Scopelarchoides signifer - S. climax - S. kreffti - Benthalbella* group represents retention of a larval character, since in all scopelarchid larvae the basihyal is elongate and teeth are restricted to the basihyal. Two states of character 4 are recognized in scopelarchids:

(0) = basibranchial teeth present, basihyal short (fig. 9)

(5) = basibranchial teeth absent, basihyal long

5. SQUAMMATION

The reduction or loss of body scales is a feature shared by all alepisauroids except the scopelarchids. In the chlorophthalmids, scopelarchids, and most myctophiform fishes, the body and postorbital regions of the head are covered with "normal" cycloid scales. The body is covered with reduced, thin, caducous scales in the Paralepidini. The body is naked (except for scales associated with the lateral line, if present) in all other alepisauroids. There is no variation in this character in scopelarchids.

6. LATERAL LINE SCALES

The presence of modified scales associated with the lateral line is typical of many myctophiform fishes. In many myctophids, chlorophthalmids, paralepidids, and scopelarchids, the lateral line scales are usually larger than adjacent body scales and each (except the last in the series) consists of a bony plate, pierced by a central pore, the latter covered or partially so by a bony tympanum. Such scales are absent in all other alepisauroids. Among scopelarchids (fig. 2) the shape and ornamentation of the lateral line scales are diagnostic for each species, and may be indicative of relationships among groups of species. States of character 6 are not defined for scopelarchids in this report.

The following four characters are "loss characters" where the loss of a feature in a group is considered to be a derived state when the presence of the feature is common in primitive teleostean fishes and widespread among groups believed related to the group in question.

7. GILL RAKERS

Normal lathlike gill rakers are typically found in myctophoid myctophiforms, but are found in no alepisauroid myctophiform (being replaced by teeth). This is, to my knowledge, the only derived state possessed by all alepisauroid fishes not seen in chlorophthalmids. The possibility of convergence among alepisauroids in the loss of gill rakers exists, since gill rakers are considerably reduced or absent among the following myctophoid myctophiforms: Synodontidae (Anderson et al., 1966, p. 31); Bathysauridae (Mead, 1966b, p. 104); *Bathytyphlops* among the Ipnopidae (Mead, 1966d, p. 147); *Centrobranchus* among the Myctophidae (Paxton, 1972, p. 24). There is no variation in this character among scopelarchids.

8. SUPRAORBITAL BONES

Supraorbital bones are present in *Aulopus*, chlorophthalmids, *Macroparalepis*, and *Rosenblattichthys*. Supraorbitals are absent in the remaining scopelarchids and (at least) in *Evermannella indica*. Two states of character 8 are recognized in scopelarchids:

(0) = presence

(6) = absence

9. ANTORBITAL BONES

Antorbital bones are present in *Aulopus*, chlorophthalmids, myctophids (Paxton, 1972), paralepidids (known for *Macroparalepis*), evermannellids (known for *Evermannella indica*), and some scopelarchids. Two states of character 9 are recognized among scopelarchids:

(0) = antorbital present

(7) = antorbital absent

10. SUPRAMAXILLARY BONES

The supramaxillary bones are large, one-third to one-fourth the length of the maxillary bone in chlorophthalmids, paralepidids, some scopelarchids, and evermannellids (known for *Evermannella indica*). Three states of character 10 are recognized in scopelarchids:

- (0) = supramaxilla large, length of supramaxilla one-fourth to one-third the maxillary length
- (8) = supramaxilla reduced to a splintlike element, less than one-ninth of maxillary length
- (9) = supramaxilla absent

11. SECOND URAL CENTRUM

Rosen and Patterson (1969, p. 365) described the primitive myctophoid (*Aulopus* and the Cretaceous *Nematonotus*) caudal skeleton as containing six hypurals, three epurals, two uroneurals, and a free second ural centrum. This is the condition in scopelarchids except that in all the second ural centrum has fused with the first ural centrum and the first preural centrum (*Benthalbella dentata* is unique among scopelarchids in possessing only two epurals). There is a free second ural centrum in chlorophthalmids, paralepidids, and evermannellids (known for *Evermannella indica*). Other than the loss of one epural in *B. dentata*, there is no variation in caudal skeleton structure among scopelarchids.

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12. ATTACHMENT OF FIRST VERTEBRA TO SKULL

In Aulopus, Synodus (Gosline et. al, 1966, p. 8), paralepidids, and all other alepisauroids other than scopelarchids the first vertebra possesses a full amphicoelous centrum attached directly to the back of the skull. In chlorophthalmids and all scopelarchids the first vertebra is a half-centrum attached to the rear of the skull through a tube of fibrous connective tissue whose length is equal to or greater than the length of the first centrum. This gap in ossification also occurs in neoscopelids (Gosline et al., 1966). There is no variation in this character among scopelarchid species.

13. MODE OF REPRODUCTION

Gonochorism is presumably the primitive mode of reproduction in myctophiform fishes, and is found (at least) in the following families: Aulopidae (Mead, 1966a, p. 21), Synodontidae (Gosline et al., 1966, p. 14), and Myctophidae (sexes are presumably also separate in neoscopelids and harpadontids). Synchronous hermaphroditism is apparently universal among the abyssal benthic families [Bathysauridae (Gosline et al., 1966, p. 14), Bathypteroidae (Mead, 1966b, p. 115), Ipnopidae (Mead et al., 1964, p. 574; Neilson, 1966)]. Synchronous hermaphroditism is universal among the Chlorophthalmidae (Mead, 1966c, p. 163) and alepisauroid myctophiforms (R. H. Gibbs, Jr., pers. comm.). R. R. Warner and I have examined representatives of all four scopelarchid genera and all species examined proved to be synchronous hermaphrodites.

14. PERITONEAL PIGMENT SECTIONS

A single dorsomedial peritoneal section is found in the larvae of *Chlorophthalmus* (Taning, 1918, p. 5) and in the species of scopelarchids possessing the greatest proportion of primitive character states (*Rosenblattichthys, Scopelarchoides signifer, S. climax,* and presumably *S. kreffti*). This, plus the fact that the changes in peritoneal pigment sections in larvae in the line leading to *Scopelarchus* are correlated with characters 1 and especially 2 on a one-to-one basis (table 10), lead me to believe that a single peritoneal section is the primitive state in the Scopelarchidae. Paralepidid larvae exhibit at least three pairs of peritoneal pigment sections (Rofen, 1966a), a higher number than found in any scopelarchid.

As states (11), (12) represent nearly ideal intermediates between state (0) and state (13), and because they correlate perfectly with states (2), (3) of character 2, five states of character 14 are recognized among scopelarchids.
Number of peritoneal sections in larvae:

(10) = 0

(0) = 1

- (11) = 3, the posterior paired sections appearing much later in development than the anterior section, and appear entirely anterior to the pelvic fin base.
- (12) = 3, the posterior paired sections appearing much later in development than the anterior section, and appear over the pelvic fin base.
- (13) = 3, the posterior paired sections appearing in near synchrony with the anterior section, and appear entirely posterior to the pelvic fin base.

15. Accessory Pigment Spots or Areas

Deep-lying pigment spots or areas are found in *Chlorophthalmus* (Tåning, 1918, p. 5) and paralepidids (Rofen, 1966a). Various patterns of these spots allow the unique recognition of each species of *Rosenblattichthys* (presumed for *hubbsi*) and *Scopelarchoides* (presumed for *kreffti*), and the general pattern of the pigment spots or areas is diagnostic for each of these genera (figs. 29, 37). The presence of deep-lying pigment spots or areas embedded in flesh is presumed to be primitive for the Scopelarchidae. Two states of character 15 are recognized among scopelarchids.

(0) = pigment spots or areas present

(14) = pigment spots or areas absent

16. METAMORPHOSIS

In this study I have defined the onset of metamorphosis in larvae to be indicated by the appearance of all peritoneal sections (or in Benthalbella by the appearance of peritoneal pigment) and the completion of metamorphosis is indicated by the formation of a complete undivided tube of peritoneal pigment around the gut. During the period between onset and completion of metamorphosis the following changes occur: elongation of the intestine bringing the anus to its adult position directly in front of the anal fin; posterior expansion of the caecum, to its adult position just before the anus; investiture of the abdominal cavity wall with muscle; appearance of head and body pigmentation; appearance of scales; appearance of gonads; in short, a change from a distinctly larval to a distinctly adult appearance. In most scopelarchids an increment of 20-40 mm. or more of growth separates the onset from the completion of metamorphosis, and the adult characteristics are acquired essentially one by one over this period of growth. This gradual metamorphosis is also apparently the case in chlorophthalmids (Taning, 1918), paralepidids (Rofen, 1966a), Omosudis (Rofen, 1966b), Alepisaurus (Rofen, 1966b), and evermannellids (Rofen, 1966d). Among scopelarchids, Scopelarchus michaelsarsi and S. stephensi begin and complete metamorphosis at a smaller size than any other scopelarchid species. Larvae of Benthalbella

undergo rapid metamorphosis after a prolonged period of growth while retaining larval form. Adult characteristics are then acquired by larvae of *Benthalbella* over a very small increment of size (fig. 18). These two extremes are recognized (for the time being) by the definition of three states of character 16 among scopelarchids.

Metamorphosis:

- (15) = gradual; onset at 12-15 mm. S.L. or smaller; completion at 30-35 mm. S.L. or smaller.
- (0) = gradual; onset at 16-20 mm. S.L. or larger; completion at 40-60 mm. S.L. [most species, *R. alatus* is extreme with onset at 9-10 mm. S.L. and not yet complete in six (39.9-80.1) juveniles examined].
- (16) = abrupt; onset at 49.6-89.1 mm. S.L. or larger; completion at 68.3-98.6 mm. S.L. or larger (size for both onset and completion of metamorphosis varies among the five species of *Benthalbella*).

17. Appearance of Pelvic Fin Bud in Larvae

Pelvic fin buds appear behind the dorsal origin in larval *Chloroph-thalmus* (Tåning, 1918), paralepidids (Rofen, 1966a), evermannellids (Rofen, 1966d), and all but four species of scopelarchids. In *Benthalbella* (except *B. macropinna*) the pelvic fin buds appear entirely anterior to the dorsal origin. Two states of character 17 are recognized in scopelarchids:

(0) = pelvic fin buds appear behind dorsal origin

(17) = pelvic fin buds appear anterior to dorsal origin

As presently understood, the following four characters are autapomorphies (Brundin, 1966, p. 25), unique, presumably derived features diagnostic of one group of species, no doubt indicative of the monophyletic origin of that group, but not (as presently defined) indicative of the phylogenetic relationships of that group (state (16) of character 16 may also belong here). These characters are included as corroboration to my recognition of *Rosenblattichthys* and *Scopelarchus* as natural groups, and are identified in Table 10 and Figure 60 by the prefix "A" before the character state integer.

18. Development of Pectoral Fin

The pectoral fins in *Rosenblattichthys* are precocious, developing prior to all other fins except the caudal and are extremelyprominent in small larvae (fig. 29). This feature is unique to larvae of *Rosenblattichthys* among scopelarchids, and is apparently not found in chlorophthalmids (Tåning, 1918) or other alepisauroids (Rofen, 1966a, b, d). Two states are recognized:

- (0) = pectoral fin not precocious, all other fins with completely differentiated rays prior to ossification of the ventralmost rays (at least) of the pectoral fin
- (A18) = pectoral fin precocious, developing completely differentiated rays prior to the formation of the complete complement of rays of all other fins (except caudal)

19. HEAD LENGTH IN LARVAE

The head in larval *Rosenblattichthys* is extremely large, deep, and massive, the head length exceeding 30 per cent of the S.L. in specimens up to 28 mm. or larger (fig. 29). The head length in other scopelarchid larvae does not exceed 30 per cent of the S.L., and this is apparently the case in chlorophthalmids (Tåning, 1918) and other alepisauroids (Rofen, 1966a, b, d). Two states of character 19 are recognized in scopelarchids:

(0) = head length in larvae not exceeding 30 per cent of S.L.

(A19) = head length in larvae (up to 28 mm. S.L.) exceeding 30 per cent of S.L.

20. HYOMANDIBULAR ARTICULATION WITH OPERCLE

A posterior, well-defined, rounded to flattened arm of the hyomandibular bone articulates with the opercle in chloropthalmids, paralepidids, evermannellids, and most scopelarchids. In all four species of *Scopelarchus* there is no discrete posterior arm of the hyomandibular bone, and the articulation of the opercle is, rather, with a rounded ridge on the posterior margin of the hyomandibular. Two states of character 20 are recognized in scopelarchids:

Discrete posterior arm of hyomandibular bone: (0) = present (A20) = absent, represented only by a rounded ridge

21. DERMAL PIGMENT STRIPES

Although dermal pigmentation and/or dermal pigment stripes are found in all scopelarchid genera except *Benthalbella*, the pattern of equal or subequal stripes above and below the lateral line is diagnostic of and unique to the four species of *Scopelarchus* (figs. 49, 54, 56, 59) among the Scopelarchidae. The fixation of one pattern in *Scopelarchus* (especially in view of the variation in such pigmentation evidenced within the genus *Scopelarchoides*) is, I believe, another indication of the relationship between the four species of *Scopelarchus*. The recognition of all patterns of dermal pigmentation (including absence) other than that found in *Scopelarchus* as primitive is, of course, artificial (for example, the loss of dermal pigment in *Scopelarchoides signifer, S. climax,* and *Benthalbella*, is presumably a derived feature shared by these species, which may or may not indicate phylogenetic relationship between them). For the present, two states of character 21 are recognized in scopelarchids:

- (A21) = dermal pigment on body as equal or subequal stripes above and below the lateral line
- (0) = dermal pigment on body not so arranged

Almost all previous authors have asserted that the scopelarchids and evermannellids are most closely related to each other and set apart from other alepisauroid families. There is a growing body of evidence that this may not be the case.

(1) Scopelarchids and evermannellids (except *Odontostomops*) have tubular eyes, yet there is a good possibility that the tubular eye of each group has been acquired independently. Munk (1966) cites a number of differences between scopelarchid and evermannellid eyes, while pointing out similarities between the eyes of *Omosudis* and evermannellids, not the least of which is that these two families have retinae composed of transmutated cones, rather than the pure rod retinae of all other deepsea families, including the scopelarchids.

Other, presumably derived, features in which evermannellids differ from scopelarchids (or at least from the primitive state in scopelarchids) include: (2) absence of parietal bones (Parr, 1929); (3) loss of suspensory pharyngobranchial, support of first epibranchial via a ligament to anterior end of third pharyngobranchial; (4) reduction in size of basihyal and basihyal tooth plate, loss of basihyal teeth; (5) loss of basibranchial teeth; (6) loss of scales; (7) loss of supraorbital; (8) eight infraorbitals, cf. six.

Derived features in which scopelarchids differ from evermannellids (and from paralepidids) include (1) basihyal completely ossified; basihyal teeth much enlarged and hooklike; (2) second ural centrum fused with first ural centrum plus first preural centrum; (3) first vertebra a halfcentrum with a gap in ossification between first centrum and skull, this gap occupied by a tube of tough fibrous connective tissue.

If it is possible to discount the tubular eyes common to each group, I know of no derived feature shared by scopelarchids and evermannellids other than the loss of gill rakers (true of all alepisauroids). I do not know the significance of the position of the anus (closer to the anal origin in scopelarchids; half-way between the pelvics and anal origin in evermannellids; closer to the pelvic insertion in chlorophthalmids (except *Bathysauropsis*) and other alepisauroids), a character used by Gosline et al. (1966, p. 17) to group the scopelarchids and evermannellids. Is closeness of the anal fin origin in Aulopidae, Bathysauridae, Myctophidae, Neoscopelidae, and Synodontidae; closer to the pelvic insertion in Ipnopidae and Notosudidae; and variable in Bathypteroidae (Anderson et al., 1966; Bolin 1966a, b; Marshall 1966; Mead, 1966a, b, c,

d, e). In larval scopelarchids the anus is initially closer to the pelvic insertion or at most half-way between the pelvic insertion and the anal origin (except *Scopelarchus* where the initial position of the anus is halfway between the pelvic insertion and the anus or closer to the anal origin), and extends posteriad with growth. Evermannellids differ from scopelarchids in an array of other features, e.g., marked enlargement of the anterior palatine fangs, position of the fins and the number of fin rays, details of the pectoral girdle, etc. I reject the notion of any close affinity between evermannellids and scopelarchids.

In addition to the loss of gill rakers, one other character apparently seen in all alepisauroids, but not in chlorophthalmids or (most) other myctophoids is the ventral insertion of the pectoral fin and the low angle (generally less than 45°) of the fin base to the longitudinal axis of the body. This latter character is discussed by Gosline et al. (1966) and Marshall (1955), and I have nothing to add to their discussion.

A derived feature shared by scopelarchids and chlorophthalmids not seen in other alepisauroids is the gap in ossification between the first centrum and the skull, discussed under character 12. There are a number of additional similarities between chlorophthalmids and scopelarchids: eyes large, directed somewhat dorsally in chlorophthalmids, distinctly tubular in scopelarchids; frontals enlarged, forming paired pored tubes in interorbital area; interorbital area narrow; dorsal insertion well ahead of midlength of body; great similarity in larval morphology, especially between *Chloropthalmus* (Tåning, 1918, p. 5) and *Scopelarchoides* (fig. 37), and including shape, position of fins, pigmentation, position of anus, etc. There exists no real evidence that the relationship of the Scopelarchidae to the Paralepidiae (or other alepisauroids) is any closer than that of the Scopelarchidae to the Chlorophthalmidae. Detailed additional study is required before the position of the Scopelarchidae within myctophiform fishes will be clearly understood.

The family Scopelarchidae is unique among myctophiform and, to my knowledge, among teleosts in the joint possession of tubular eyes and the peculiar, strong, straight-to-strongly-hooked lingual teeth, present over the basihyal, present or absent over the basibranchials. Among the chlorophthalmid-alepisauroid fishes, scopelarchids are apparently distinguished in the fusion of the second ural vertebra with the first ural vertebra and the first preural vertebra (I do not know the state of this character in alepisauroids other than the paralepidids examined and *Evermannella indica*), the complete ossification of the large basihyal, the distinctive large larvae, the adult position of the anus, and various other details. There is little doubt that the Scopelarchidae is a natural group. The purpose of the remaining discussion in this section is twofold: first, to add to the short list of characters presented as Table 10, in an effort to defend my division of the Scopelarchidae into four genera; and, second, to develop the thesis that the genera *Scopelarchus* and *Benthalbella* represent separate endpoints of scopelarchid evolution; that each of these genera is rather easily defined by the comparatively large number of derived features shared by each of their respective groups of species; and that the view presented of the relationships between species of each of these lineages agrees well with the zoogeographic analyses presented in the last section of this paper.

There are two groups of scopelarchid species exhibiting the smallest proportion of derived character states (table 10); Rosenblattichthys and three species of Scopelarchoides: signifer, climax, and kreffti (some osteological features are presumed for R. alatus, R. hubbsi, S. climax, and S. kreffti; some larval features are presumed for R. hubbsi and S. kreffti). These species exhibit the presumably primitive states of the following characters: 1—parietals present; 2—suspensory pharyngobranchial present; 9—antorbital present; 10—supramaxilla large; 14—a single peritoneal section; 15—accessory pigment spots or areas present; 16—metamorphosis gradual; 17—pelvic fin bud appears posterior to dorsal origin. In addition, Scopelarchoides signifer, Rosenblattichthys alatus, and R. volucris agree in the following characters:

- **a.** Larvae short-bodied, deep, with pelvic fins appearing behind dorsal base on midlateral abdominal cavity wall (also true for *S. climax*).
- b. Opercle plow-share shaped, smaller than subopercle.
- c. Interopercle Z-shaped (not known in *R. alatus;* interopercle in the form of an inverted L in all other scopelarchid species examined).
- d. Vertebrae: S. signifer, 16 + 32 = 48, range = 48-49; R. alatus, range = 46-47; R. volucris, 16 + 33 = 49, range 49-51.
- e. Lateral line scales: S. signifer, range = 49-52; R. alatus, range = 47-48; R. volucris, range = 48-51.

These characters may also be primitive for the family. The only known derived features shared by *Rosenblattichthys* and the three species of *Scopelarchoides* listed above, are those features shared with all other scopelarchids.

The three species of *Rosenblattichthys* share the presumably derived states (A18) of character 18—pectoral fin development precocious in larvae; and state (A19) character 19—head in larvae notably enlarged, deep, and massive; head length exceeding 30 per cent of the S.L. in larvae up to 28 mm. S.L., and in these two characters are unique among scopelarchids. Differences between *Rosenblattichthys* (osteological characters based on *R. volucris* and *S. signifer*) and *Scopelarchoides* also include:

- a. Dermal pigment areas large, those in middorsal and midventral contour of body anterior to end of adipose dorsal and anal fin bases, respectively, cf. dermal pigment areas as small discrete spots or bars, those in middorsal and midventral contour of body posterior to end of dorsal adipose and anal fin bases, respectively (except IA when present).
- **b.** Interorbital area broad [interorbital width 3.2 (2.8-4.7) per cent S.L. in *R. volucris*], cf. interorbital area narrow [interorbital width 1.8 (1.4-2.4) per cent S.L. in *S. signifer*].
- c. Supraoccipital with crest extending full length of bone, cf. supraoccipital with a spikelike or knoblike spine.
- d. Ethmoid process on first infraorbital (fig. 5) absent, cf. present.
- e. Distinctive differences in lateral line scale shapes (fig. 2).
- f. Three extrascapulars, cf. two.
- **g.** Pelvic fin insertion in adults slightly anterior to dorsal origin, cf. pelvic fin insertion in adults under anterior one-third of dorsal base (except *S. kreffti*, where slightly anterior to dorsal origin).

These characters convince me that the species of *Rosenblattichthys* represent an early dichotomy in the evolutionary history of the Scopelarchidae, and that, on the whole, the genus *Rosenblattichthys* could be described in Hennig's (1966) terminology as the plesiomorph sister group of the remaining scopelarchids. The three known species of *Rosenblattichthys* agree remarkably well in meristic, morphometric, osteological, and larval features and, I am convinced, form a natural group.

The remaining scopelarchids: species of *Scopelarchoides, Scopelarchus*, and *Benthalbella*; share only one derived feature [character 8, loss of supraorbital] not also found in *Rosenblattichthys*, although I am convinced others will be found. An apparent early division into two lineages can be recognized in this group of species, one lineage leading to *Scopelarchus*, the other to *Benthalbella*.

Among this group, Scopelarchoides signifer (and presumably S. climax and S. kreffti) exhibit the largest proportion of presumably primitive character states (Table 10 and listed in the discussion above). Scopelarchoides nicholsi and S. danae agree with Scopelarchoides signifer but not Scopelarchus in the following characters: 9—antorbital present; 15 accessory pigment spots present, and in lacking the features unique to Scopelarchus (characters 20 and 21). S. nicholsi and S. danae also agree with S. signifer in the following characters:

a. Ethmoid process on first infraorbital present (fig. 5). This process is present in *Scopelarchoides signifer, S. danae, S. nicholsi* and *Scopelarchus,* but absent in *S. climax, S. kreffti, Rosenblattichthys,* and *Benthalbella.* The presence of this process is probably a primitive feature.

- b. Coracoid widely expanded with coracocleithral fenestra correspondingly small (apparently true of all scopelarchids except *Benthalbella*).
- c. An anteroventrally directed process on opisthotic (intercalar) reaches or nearly reaches border of prootic (apparently true of all scopelarchids except *Benthalbella*).
- d. Lack of pigment on pectoral fin (absent in Scopelarchoides signifer, S. nicholsi, S. danae, and Scopelarchus guentheri; present in Scopelarchoides climax, S. kreffti, Scopelarchus analis, S. michaelsarsi, and S. stephensi).
- e. Number of vertebrae. All species of *Scopelarchoides* and *Scopelarchus* (except *Scopelarchoides kreffti* with 55-57, and *Scopelarchus michaelsarsi* and *S. stephensi* with 40-44) have 44-51 vertebrae (there are 46-51 in *Rosenblattichthys* and 54-65 in *Benthalbella*).

In derived states of four characters [1-loss of parietals, 2-shift in support of first epibranchial, 10-reduction in size of supramaxilla, 14possession of three peritoneal pigment sections] Scopelarchoides nicholsi and S. danae agree with Scopelarchus and disagree with Scopelarchoides signifer. Three of these: 1-loss of parietals, 2-shift in support of first epibranchial, 14-possession of three peritoneal pigment sections, are unique to this lineage among scopelarchids, and two characters (2, 14) are, to my knowledge, unique among myctophiform fishes. In characters 2 and 14 S. nicholsi and S. danae possess character states ideally intermediate between the state in S. signifer and the state in Scopelarchus. The support of the first epibranchial dorsally is through a suspensory or first pharyngobranchial, and short to elongate arms at about midlength on the first epibranchial and the second pharyngobranchial are connected by a ligament in most myctophiform fishes including most scopelarchids (see discussion of character 2 and figs. 10, 11). In S. nicholsi the suspensory pharyngobranchial is lost but hooklike projections on the first epibranchial and second pharyngobranchial (connected by a ligament) remain, and the support of the first epibranchial is shifted to the medial end of the second pharyngobranchial. In S. danae the hooklike projections are lost, and support of the first epibranchial is at the middle of the second pharyngobranchial. In Scopelarchus support of the first epibranchial is at the point of articulation between the second pharyngobranchial and the second epibranchial.

Only a single peritoneal section is found in *Scopelarchoides signifer*, S. climax, Rosenblattichthys, and Chlorophthalmus agassizi (Tåning, 1918). Only a single section is found in smaller larvae of S. nicholsi and S. danae, but in these two species the onset of metamorphosis is signaled by the appearance of two additional paired sections, entirely anterior to

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(S. nicholsi) or over (S. danae) the pelvic fin base. In Scopelarchus all three sections appear early in development, and the two posterior sections are shifted to the rear of the abdominal cavity, entirely behind the pelvic fin base.

In addition to the fact that S. danae exhibits states of characters 2 and 14 morphologically intermediate between S. nicholsi and Scopelarchus, the great expansion of the opercle in S. nicholsi, the wide gap between the opercle-subopercle and the preopercle, as well as the unique distribution of this species (fig. 45) strongly suggest that the ancestor of S. nicholsi diverged from the line leading to S. danae and Scopelarchus prior to the divergence of the ancestors of S. danae and S. guentheri.

In addition to the changes in characters 2 and 14 described above, Scopelarchoides danae and Scopelarchus guentheri are quite similar in a number of other characters that suggest relationship between the two species.

- a. Opercle greater in size than subopercle (true in *Scopelarchus, S. danae*, and especially *S. nicholsi*; the opercle is equal to or less than the subopercle in size in all other scopelarchids).
- **b.** Opercle basically rectangular with vertical dimension greater than horizontal dimension (unique to *S. danae* and *Scopelarchus* among scopelarchids).
- c. Gill covers closely attached to preopercle in *S. danae* and *Scopelarchus* (fig. 8D). A wide gap between gill covers and preopercle in other scopelarchids (fig. 8A, E).
- d. Number of anal rays: S. danae, 24-27; S. guentheri, 24-29. Number of lateral line scales: S. danae, 50-52; S. guentheri, 47-52. Number of vertebrae: S. danae, 18 + 31 = 49, range = 48-50; S. guentheri, 18 + 29 = 47, range = 46-51.
- e. Great similarity in shape of lateral line scales, especially the extreme depth of the tympanum (fig. 2).
- f. The early reabsorption of most of the dorsal adipose fin, resulting in essentially adult proportions of this fin in specimens 20-22 mm. S.L. in size and larger (also true of other species of *Scopelarchus*); in *Scopelarchoides nicholsi, S. signifer,* and *?S. climax,* the dorsal adipose fin in larvae remains elongate, to over anterior anal rays, throughout metamorphosis, assuming adult proportions in specimens 40-50 mm. S.L. (*S. nicholsi*), 30-35 mm. S.L. (*S. signifer*), and remaining elongate in specimens at least 33.5-36.5 mm. S.L. (*S. climax*).

The four species of *Scopelarchus* share derived states of four characters that are unique among scopelarchids: 2—support of first epibranchial at point of articulation of second pharyngobranchial with second epibranchial; 14—possession of three peritoneal sections, the posterior paired sections appearing in near synchrony with the anterior section and appearing entirely behind the pelvic fin base; 20—loss of posterior arm on hyomandibular; 21—possession of equal or subequal dermal pigment stripes above and below the lateral line. The four species of *Scopelarchus* share an additional two derived states not found in any species of *Scopelarchoides*; 9—loss of antorbital; 15—lack of accessory pigment spots or areas.

Scopelarchus guentheri possesses a number of features whose state is probably ancestral to the state in other species of Scopelarchus:

- **a.** S. guentheri alone among the species of this genus lacks pigment on
- the pectoral fin (= Scopelarchoides danae, S. nicholsi, and S. signifer).
- **b.** S. guentheri possesses a splintlike supramaxilla (= S. danae, S. nicholsi, character 10).
- c. S. guentheri exhibits an exceedingly deep tympanum on lateral line scales above the anal origin (fig. 2) as does S. danae.
- **d.** S. guentheri is the most elongate of all species of Scopelarchus, possessing the most vertebrae and lateral line scales.

Scopelarchus analis is intermediate between S. guentheri and the two remaining species of Scopelarchus (michaelsarsi and stephensi) in number of vertebrae, lateral line scales, and anal fin rays; in the variability of pigment on the pectoral fin; and in size at metamorphosis (character 16), with onset in S. analis at 17-20 mm. S.L. and completion at 45-55 mm. S.L. (in S. michaelsarsi and S. stephensi, onset at 12-15 mm. or less, completion at 30-35 mm. or less).

The reduction in number of vertebrae and lateral line scales and the earlier onset of metamorphosis in *S. michaelsarsi* and *S. stephensi* may be correlated characters, and may be related to the common habitat of both species (fig. 58) within low-productivity central portions of the central gyrals. Reduction in body size and number of vertebrae has been noted for other fishes living in the central water masses (e.g., Ebeling, 1962, pp. 145-146). If the reduction in body size, numbers of vertebrae, numbers of lateral line scales, and earlier onset of metamorphosis are correlates of the common environment of *S. michaelsarsi* and *S. stephensi*, then the information content of these characters regarding the phylogenetic relationship of these two species is uncertain. There is no other evidence at present that these two species are more closely related to each other than either of them is to *S. analis*.

That *Scopelarchus* is a natural group is indicated by the following features, which in combination uniquely define the genus: frontals greatly expanded, occupying at least one-half of postorbital dorsal roof of skull (unique among scopelarchids); parietals absent; antorbital absent; no ethmoid process on first infraorbital; prong-like projection on second

infraorbital excluding third infraorbital from posteroventral angle of infraorbital series; support of first epibranchial at joint of second pharyngobranchial and second epibranchial (unique among scopelarchids); opercle rectangular, nonserrate, deeper than subopercle; 40-52 lateral line scales; 40-51 vertebrae; 18-22 pectoral rays; equal or subequal stripes of dermal pigment above and below lateral line (unique among scopelarchids); epidermal pigment limited to dorsal to lateral line; pectoral fin exceeding pelvic fin in length (otherwise true only in *Scopelarchoides signifer*); pelvic insertion beneath or behind middle of dorsal base; pelvic fin bud in larvae appears ventrolaterally, at or below level of intestine, beneath or behind dorsal base; three peritoneal pigment sections, the posterior pair appearing far behind the pelvic fin base (unique among scopelarchids); no accessory pigment spots or areas.

In turning to the other major lineage in the Scopelarchidae, that leading to Benthalbella, it is necessary to draw the limits of the genus Scopelarchoides. Scopelarchoides signifer, S. climax, S. kreffti, and Benthalbella share one presumably derived feature not found in other scopelarchids: state (5) of character 4-basibranchial teeth absent, lingual teeth occurring only over elongate basihyal. There exist no derived features that I am aware of that are shared uniquely by the five species included in the genus Scopelarchoides. The genera Rosenblattichthys. Scopelarchus, and Benthalbella, are all defined by a number of presumably derived features, unique as far as known, to the members of each of these respective taxa. This leaves the genus Scopelarchoides whose members are associated, at present, only by a lack of derived features defining the other genera. On the basis of evidence presented herein it might be argued that Scopelarchoides nicholsi and S. danae be united with Scopelarchus, whereas S. signifer, S. climax, and S. kreffti, be united with Benthalbella, thus eliminating the problem. To my mind such a procedure would destroy the significance of Scopelarchus and Benthalbella as taxa.

Despite the mosaic of primitive and derived features exhibited by the five species of *Scopelarchoides*, I have united them under one name for the following reasons:

First, the phyletic analysis presented here is both primitive and preliminary. Additional information may reinforce the compromise adopted here, it may also force the recognition of additional taxa, but in the interests of a balanced classification, I would want to see additional evidence before attempting the description of an additional genus.

Second, the genus *Scopelarchoides* can be clearly diagnosed in terms of available information, not only by the array of characters its members do not possess but also by the pattern of accessory pigment spots unique to this genus among scopelarchids (although this may be a primitive feature).

l know of no derived features shared by *Scopelarchoides signifer*, *S. climax*, or *S. kreffti* not also seen in *Benthalbella*. This is probably due to lack of information (osteology unknown in *S. climax* and *S. kreffti*, larvae unknown for *S. kreffti*).

Larvae of S. climax are virtually identical to those of S. signifer (fig. 37), sharing at least the following (probably primitive) features: only one peritoneal section; appearance of pelvic fin buds beneath or behind dorsal base, in midlateral abdominal cavity wall, well above level of intestine; accessory pigment spots present; dermal pigmentation absent (this may be a derived feature which may set S. signifer and S. climax apart from all scopelarchids except Benthalbella). S. climax also agrees with S. signifer in the following characters: antorbital present; supramaxilla large: identity of shape of second and third infraorbitals; meristic characters; insertion of pelvic fin under anterior one-third of dorsal base. Characters exhibited by S. climax that are probably derived with respect to the state in S. signifer include: rearward displacement of single peritoneal section (unique among scopelarchids); decreased number of accessory pigment spots, to one, (unique among Scopelarchoides, but larvae of S. kreffti are unknown); uniform pigmentation of body and fins (similar to *Benthalbella*); and lack of an ethmoid process on first infraorbital (= Benthalbella).

Scopelarchoides kreffti was included in this genus because of the following features it shares with S. signifer and S. climax:

- a. Antorbital present (absent in all Benthalbella except B. macropinna).
- **b.** Dermal pigment stripes present (absent in *S. signifer, S. climax,* and *Benthalbella,* but present in *S. danae* and *S. nicholsi*).
- c. Near identity of second and third infraorbitals in relative size and shape with those in S. signifer and S. climax.
- d. Weak serration of opercle (also true of S. signifer and S. danae).
- e. Similarity of lateral line scale shape (fig. 2), especially the extremely deep tympanum.

Scopelarchoides kreffti differs from all other scopelarchids except Benthalbella in the numbers of vertebrae and lateral line scales (S. kreffti, vertebrae 55-57, lateral line scales 58-59; Benthalbella, vertebrae 54-65, lateral line scales 54-66; other scopelarchids, vertebrae 40-51, lateral line scales 40-53). S. kreffti also agrees with Benthalbella in the forward insertion of the pelvic fins in adults, slightly anterior to dorsal origin (far ahead in Benthalbella, slightly ahead in Rosenblattichthys, behind in Scopelarchus and other Scopelarchoides) and in the probable presence of luminescent organs (otherwise known to be present only in *B. infans*). I expect that larvae of *S. kreffti* will exhibit the following features: a single peritoneal pigment section (such sections absent in *Benthalbella*); accessory pigment spots (absent in *Benthalbella*); appearance of pelvic fin bud posterior to dorsal origin, midlaterally in abdominal cavity wall (anterior to dorsal origin (except *B. macropinna*) and ventrolaterally in abdominal cavity wall in *Benthalbella*).

The five species of *Benthalbella* share two derived character states unique to them among scopelarchids: character 14—absence of peritoneal pigment sections; 16—metamorphosis abrupt; onset at 49.6-89.1 mm. S.L. or larger, completion at 68.3-98.6 mm. S.L. or larger; and also share character 15—accessory pigment spots or areas absent (table 10). Larvae of *Benthalbella* species lack dermal pigmentation (unique to *Benthalbella* except for *Scopelarchoides signifer*, and *S. climax*). The larvae of all five metamorphose at an extremely large size.

The shape and relative size of the infraorbital bones divides this genus into three groups: *B. macropinna*, similar to *Scopelarchoides signifer*, *S. kreffti*, and *S. climax; B. dentata* with a greatly expanded second infraorbital and uniquely lacking a shelf on the dorsal margin of this bone; and the three species *B. infans-B. linguidens-B. elongata* in which the second infraorbital is similar in shape to that in *Scopelarchoides signifer-S. climax-S. kreffti*, but is expanded posteroventrally and excludes the third infraorbital from the posteroventral angle of the infraorbital series (as in *S. nicholsi* and *S. danae*).

Benthalbella dentata, B. elongata, B. infans, and B. linguidens differ from B. macropinna in three presumably derived character states: 9 loss of antorbital; 10—reduction in size of supramaxilla; 17—appearance of pelvic fin bud anterior to dorsal origin (unique to these four species among scopelarchids). B. macropinna shares with B. dentata the presence of scattered melanophores on the pectoral fin prior to (but not after) the ossification of the pectoral fin rays. The elongate anal fin of B. macropinna is unique.

B. dentata possesses at least six presumably derived features unique to itself among scopelarchids:

- **a.** Sixth infraorbital (dermosphenotic) extends nearly to lateral wall of infraorbital area.
- **b.** Second infraorbital greatly expanded, a shelf on dorsolateral margin lacking.
- c. Great expansion of subopercle, subopercle considerably larger in size than opercle.
- **d.** Dorsal adipose fin base lies entirely posterior to a vertical through base of last anal ray.

e. Pectoral fins minute.

f. Two epurals.

Benthalbella elongata, B. infans, and B. linguidens share one feature that sets them apart from all other scopelarchids—the shape of the lateral line scales above the anal origin is similar in all three (fig. 2) and distinct from all other scopelarchid species, e.g., the H/L ratio is less than 1.00 in all three and greater than 1.00 in all other scopelarchids (except one (103.5) specimen of Rosenblattichthys volucris where H/L = .940). In addition, these three species exhibit great similarity in morphometric characters, the larvae of all three are virtually identical in morphology, and all three are set apart by a distinctive shape of the second infraorbital and a distinctive relationship of the third infraorbital to the second unique to these three species among scopelarchids (fig. 5B).

Although I know of no characters clearly giving evidence for the relationship of any of these three with respect to one another. I had no doubt that these three species were more closely related to each other than any of them to any other scopelarchid species. The discovery of ventral luminescent organs in B. infans (Merrett et. al. 1971) and its probable presence in Scopelarchoides kreffti, but its apparent lack in all other species of *Benthalbella*, throws serious doubt on the common origin of Benthalbella. In weighing evidence available to me, I consider it highly unlikely that the high degree of similarity between B. infans-B. linguidens-B. elongata is due to convergence. Further, the unique derived features shared by the larvae of all species of *Benthalbella* bespeak a common origin. In the absence of further evidence, to base the classification of this genus entirely upon the known presence of luminous tissue in B. infans and the unknown state of this character in other species of Benthalbella, would create an unwieldy and imbalanced classification. For, if the difference between B. infans vs. B. linguidens-B. elongata is at the generic level, then so are the differences between these two groups and B. macropinna, on the one hand, and B. dentata, on the other. Also, if the presence of luminous tissue justified the recognition of a separate genus to include only B. infans, then it would also be sufficient for such recognition for S. kreffti. This one character, if used to recognize a separate genus for B. infans, would force the recognition of five genera to contain six species (four of the genera would be new). I think it likely that luminous tissue will be found in other species of Benthalbella since the nature of the luminous tissue, apparently derived from muscle tissue, could easily result in diffuse not easily visible organs.

My view of the relationships between scopelarchid species is presented as Figure 60.

ZOOGEOGRAPHY AND EVOLUTION

A major benefit derived from systematic studies of midwater organisms is the ability to compare the distributions of species of different taxonomic groups. A growing body of literature dealing with invertebrates and vertebrates of the oceanic habitat demonstrates that recurrent patterns of distribution are found from group to group, and that similarities in distributional patterns exist between groups as disparate as phytoplankton and epipelagic fish, copepods, squid, and midwater fishes.

A great number of physical and biological features of the oceanic environment have been used to explain the observed distributions of various species (summaries of factors thought to be important are provided by Brinton, 1962; Ebeling, 1962, 1967; Johnson and Brinton, 1963; Bussing, 1965; Parin, 1968; Frost, 1969; Craddock and Mead, 1970; Ebeling et al., 1970; Knox, 1970; McGowan, 1971 among others). Included among these factors are the following: currents, including confinement of indigenous populations by gyral systems, and the boundary effects of convergences and divergences (Bruun, 1958; Wisner, 1959; Ebeling, 1962; Reid, 1962; Wickett, 1967; Frost, 1969); temperature (Clarke, 1950; Brinton, 1962; Nafpaktitis, 1968); density (Pickford, 1946); oxygen (David, 1963; Mead, 1963; Gibbs and Hurwitz, 1967; Longhurst, 1967a); biological productivity or some measure of available food supply (Bogorov, 1958; Ebeling, 1962; King and Iversen, 1962; Roper, 1969); and water masses (Bary, 1959; Bronton, 1962; Ebeling, 1962, 1967; Ebeling et al., 1970; McGowan, 1971; among others).

Water masses are defined by their temperature-salinity characteristics, and identified by the consistency of the temperature-salinity relationships throughout the extent of the water mass (Sverdrup et al., 1942, pp. 142-143). The water mass hypothesis, i.e., the association of the distribution of oceanic animals with water masses, has been discussed in detail in most of the literature concerned with the biogeography of the open ocean. The water mass concept is useful in drawing boundaries in the sea between waters of different physical (T-S), chemical (e.g., O_2), and biological properties. The distributions of a large number of species have been shown to correspond closely to a given water mass or water masses (e.g., chaetognaths: Bieri, 1959; Sund, 1959; euphausiids: Brinton, 1962; sergestids: Judkins, pers. comm.; pelagic tunicates: Berner, 1957; pteropod molluscs: McGowan, 1960a, 1963; *Poeobius:* McGowan, 1960b; squid: Wormuth, 1971; midwater fishes: Aron, 1959, 1962; Ebeling, 1962, 1967; Becker, 1964; Backus, Mead et al., 1965; Paxton, 1965, 1967; Gibbs and Hurwitz, 1967; Lavenberg and Ebeling, 1967; Gibbs, 1968, 1969; Backus, Craddock et al., 1969, 1970; Wisner, 1970; among others).

The water mass concept is useful but obviously insufficient. It is doubtful for example that the shape of the T-S curve, defining the water mass, provides a causal explanation for the distribution of oceanic animals in most cases, if indeed in any case. For most species adult tolerances no doubt extend well beyond the T-S values found within the range of the species, although temperature may, in some cases, limit the distribution of larvae (Ushakov, 1964).

There exists the growing belief that biological interaction is an exceedingly important factor in maintaining recurrent patterns of distribution. The concordance in distributions of oceanic species from many taxonomically distinct groups has suggested that the oceanic fauna is organized into recurrent assemblages of organisms, i.e., communities, and that these communities have structure in the sense that the constituent species are coadapted to each other's presence, and that each species plays a specific role in the flow of energy and recycling of materials through the community (Margalef, 1958, 1963, 1968; Fager and Mc-Gowan, 1963; McGowan, 1971). The definition and study of these communities in the open ocean is an exceedingly complex problem, yet increased knowledge of oceanic communities should certainly lead to a better understanding of the patterns of distribution of oceanic species. A feature of major interest derived from systematic study of the Scopelarchidae is that it is a group of large-bodied midwater predators consisting of species whose distributions are similar to the distributions of many other smaller-bodied midwater fishes, nektonic invertebrates, and planktonic groups.

Brinton (1962), Ebeling (1962), McGowan (1971), and others have classified the distributional patterns exhibited by midwater animals into essentially three categories:

1. Those species limited to part or all of one water mass, including those species limited to areas transitional between water masses.

2. Those species whose distributions cross water mass boundaries, inhabiting either adjacent, physically and biologically similar water masses, or showing wide disjunctions in distribution.

3. Those species limited to nearshore waters.

Of the 17 known species of scopelarchids, two, *Rosenblattichthys hubbsi* and *Scopelarchoides climax*, are known from a very small number of specimens (one and eight respectively) and are each known only from an extremely limited geographic locality.

Of the 15 species whose distributions can be characterized, eight species appear to be limited to all or part of one water mass, while seven species cross water mass boundaries.

Most of the species limited to all or part of one water mass area are from the central and eastern Pacific, where large intrinsic (TS, etc.) differences between water masses are perhaps emphasized by regional variations in biological productivity, upwelling, oxygen etc.

Scopelarchoides nicholsi (fig. 45) is limited to those areas of the Pacific Equatorial Water Mass exhibiting the greatest development of a subsurface layer of poorly oxygenated water. The distribution of this species is disjunct, as shown in Figure 45, with a northern area extending from ca. 27° N to 5-9° N and west to 136° W, and a southern area off Peru extending from 6° S to 12-13° S and west to ca. 87° W, but S. nicholsi does not occur in the intervening equatorial area. This region is occupied by Rosenblattichthys volucris and Scopelarchus guentheri (figs. 36, 55).

S. nicholsi is thus endemic to portions of the eastern tropical Pacific, an area noted for the distinctness of its fauna. Ebeling (1967, p. 602) classified this area as a primary faunal region with less than 17 per cent of its reported deepsea fauna occurring throughout adjacent central and transitional waters. Among groups known to contain species endemic to this area are a large number of invertebrate taxa: chaetognaths (Bieri, 1959), euphausiids (Brinton, 1962), squid (Wormuth, 1971), and sergestid shrimp (Judkins, pers. comm.). A large number of midwater fishes, spanning the phylogenetic spectrum of deepsea groups, are endemic to this area: *Talismania bifurcata* (Ebeling, 1967), *Bathophilus filifer* (Barnett and Gibbs, 1968), *Chauliodus barbatus* (Morrow, 1961), *Stomias colubrinus* (Gibbs, 1969), a number of myctophid and paralepidid species (Rofen, 1966a); *Melamphaes laevicips, M. spinifer* (Ebeling, 1962), and a number of ceratioid anglerfishes (Bertelsen, 1951); among others.

The equatorial region of the eastern Pacific is complex hydrographically, and its regional character is maintained by zonal flow of equatorial currents and countercurrents, formation of Pacific Equatorial Water by subsurface mixing processess, a shallow thermocline, high productivity, upwelling, and a pronounced subsurface core of waters low in dissolved oxygen content (Sverdrup et al., 1942; Brandhorst, 1959; Brinton, 1962; Ebeling, 1962, 1967; Wyrtki, 1964, etc.). Brandhorst (1959) diagrammed the geographic location of the main areas of poorly oxygenated subsurface waters, water with an oxygen content less than 0.15 ml/l below the thermocline. In Brandhorst's diagram two main areas of low oxygen subsurface waters are pointed out: a northern area extending from near Cabo San Lucas (ca. 23° N) south to 5-9° N and west to 140° W or more, and a southern area off Peru from 3-5° S to a southern endpoint not illustrated, and west to 95-100° W. These regions are enclosed by the stippling on Figure 45. The correspondance between the distribution of *S. nicholsi* and these two areas with poorly oxygenated subsurface waters is remarkable.

Despite numerous collections made within the area of occurrence of *S. nicholsi*, this species is the only species to have been captured. It is difficult to suggest other physical or biological factors that might play a more important role than oxygen in the determination of the distribution of *S. nicholsi*, e.g., the distribution of temperature (Brinton, 1962, pp. 71-73) or biological productivity (Fleming and Laevastu, 1956 reproduced in Ebeling, 1962, p. 146) does not divide this region into two clearly disjunct but similar areas as does the distribution of oxygen content. Yet the distribution of *S. nicholsi* is disjunct, and *R. volucris* and *Scopelarchus guentheri* do occur in the intervening area.

Although a number of other oceanic species exhibit patterns of distribution similar to the three forementioned scopelarchids, perhaps the clearest parallel is with the euphausiids *Euphausia eximia*, with a distribution similar to *S. nicholsi*, *E. gibboides*, partly similar in distribution to *R. volucris*, and a number of euphausiids (*Thysanopoda orientalis*, *Nematoscelis tenella*, etc.) similar to the Pacific distribution of *S. guentheri*, at least in part (Brinton, 1962). Although Brinton explained the peculiarities of the distributions of *E. eximia* and *E. gibboides* as due to "small (but ecologically significant) temperature differences between habitats," I think that these distributions might more reasonably be related to oxygen content.

A line of evidence corroborating the importance of oxygen in the determination of the distribution of *S. nicholsi* lies in the length and complexity of the gill filaments of *S. nicholsi*. *S. nicholsi* has extremely long, dense gill filaments extending posterior to the margin of the gill covers and overlapping the base of the pectoral fin. The only other scopelarchid known to me that exhibits similarly elongate gill filaments of this species are rather elongate in specimens taken throughout its distribution, but especially so in the northern Indian Ocean). The northern Indian Ocean is another area with a marked subsurface core of

poorly oxygenated water, and like the eastern Pacific, its fauna exhibits a degree of distinctness. *Chauliodus pammelas*, endemic to this area, replaces the widespread species *Chauliodus sloani* (which occurs in the southern Indian Ocean as well as in the Atlantic and Pacific). *Chauliodus pammelas* exhibits longer gill filaments with more numerous lamellae than *C. sloani* (Gibbs and Hurwitz, 1967). *Chauliodus barbatus* replaces *C. sloani* in the eastern tropical Pacific, but to my knowledge no one has compared the gill filament lengths of the two species. However, several other eastern Pacific species living in the oxygen minimum areas are known to have enlarged gill surface areas relative to congeners living outside of these areas (Ebeling, 1967).

The close correspondance of the distribution of *S. nicholsi* with the areas with subsurface waters poorest in oxygen content, the corroboration through similarity to the distribution of other oceanic species and through a morphological change best interpreted in terms of oxygen content of the environment, and the negative evidence provided by the distribution of species avoiding areas of poorly oxygenated water (e.g., *R. volucris*), leads me to conclude that oxygen is the most important factor delimiting the distribution of this species. Whether other scopelarchids are excluded from these areas of the eastern Pacific merely by the low oxygen content, or also by the presence of *S. nicholsi* in these areas of the northern Indian Ocean suggests that competitive exclusion cannot be disregarded as an explanation.

Rosenblattichthys volucris (fig 36) occurs in Transition Water off southern California and Baja California, and perhaps off Chile, as well as in a narrow zone along the equator; between the two portions of the range of Scopelarchoides nicholsi. The complex hydrography of the California Current area off the west coast from ca. 40° N to 23° N led Sverdrup et al. (1942, p. 740) to apply the term Transition Region to this area. Particularly off southern California the current systems and hydrography are complex, marked by input of water from the Pacific Subarctic, Western North Pacific Central, and via poleward subsurface intrusion, Pacific Equatorial water masses. Complex eddy systems, surface and subsurface seasonal and permanent countercurrents, and seasonal upwelling characterize this area. The fauna off southern California reflects the mixed nature of its environment, with boreal, central, equatorial, as well as endemic components (Ebeling, 1962; Ebeling et al., 1970; Lavenberg and Ebeling, 1967; Paxton, 1967). Off southern California R. volucrus is found only in this transitional region.

Along the equator *R. volucris* is found in a narrow band from 140° W to the South American mainland, and between ca. 6° N and 3° 12' S,

thus bisecting the range of *S. nicholsi.* Divergence of surface currents at the equator (more marked in the eastern Pacific than in the western Pacific) result in upwelling, a consequent weakening of the thermocline, and an increased opportunity for mixing across the thermocline (Knauss, 1963, p. 244). This results in the disjunct distribution of areas with strongest development of oxygen poor waters as mentioned above, with the main regions of oxygen poor water not extending across the equator, but occurring in large areas to the north and south as indicated in Figures 36 and 45 by the stippling. *R. volucris* and *S. guentheri* have been taken in Pacific Equatorial Water only along the equator, between these two large regions of oxygen-poor water.

The existence of the subsurface Cromwell Current (Knauss, 1963) which extends along the equator from at least 150-160° E to the Galapagos (90° W) or possibly farther eastward, provides not only a possible trans-Pacific pathway for fish species, but may, in conjunction with the westward flowing South Equatorial Current at the surface, provide a possible mechanism for populations dwelling within these currents to maintain position through differences in vertical distribution between young and adult stages, or diurnally.

The area off Chile from which R. volucris was reported by Craddock and Mead (1970) is another well-known transitional area with hydrological properties analogous in many respects to the transition region of the North Pacific.

Although numerous examples exist of wide-ranging species exhibiting avoidance of the low-oxygen areas of the eastern Pacific (e.g., *S. guentheri*), there are few species known to me distributed in a fashion similar to *R. volucris*. Among species showing similar distributions over at least part of their ranges are the following: *Euphausia gibboides* (Brinton, 1962, p. 204), *Stomias atriventer* (Gibbs, 1969, p. 15), and questionably *Lampanyctus ritteri* (Paxton, 1967, p. 429).

Thus the habitat of *R. volucris* appears to be in mixed or transitional waters characterized by complicated current systems with eddies, countercurrents and upwelling, a relatively weak or seasonal thermocline structure, and relatively high productivity and oxygen content.

Benthalbella linguidens appears to be limited to Pacific Subarctic waters (fig. 19). The distribution of *B. linguidens* as currently understood corresponds well with a number of oceanic species known to be limited to the Pacific Subarctic, and not following the course of the California Current southward into the Transition Region: euphausiids, *Thysanoessa inermis, T. longipes, Tessarabrachion oculatus* (Brinton, 1962, p. 199); chaetognaths, *Sagitta elegans, S. maxima* (Bieri, 1959, pp. 6, 18); and a

substantial number of other planktonic species ranging from Radiolaria, Annelida, Copepoda, Pteropoda to Gymnosomata (McGowan, 1971, pp. 14-17); myctophids, *Lampanyctus jordani, Protomyctophum thompsoni, Stenobranchius nanochir, Tarletonbeania taylori* (Wisner, 1959, 1970; Rass, 1960; Becker, 1963). Although the Transition Region off California is one of the best-sampled areas in the world (at all depths), *B. linguidens* has not been found south of 44.5° N.

Benthalbella dentata (fig. 19), on the other hand, appears to be a Transition Region species, following the course of the California Current southward and occurring to off Guadalupe Island, Mexico (29° 12.1-13.8' N). The distribution of *B. dentata* is similar to that of numerous other oceanic organisms: euphausiids, *Euphausia pacifica* (Brinton, 1962, p. 199); pteropods, *Limacina helicina* (McGowan, 1963, p. 114); and the myctophid fishes *Diaphus theta, Lampanyctus ritteri, Stenobranchius leucopsaras, Tarletonbeania crenularis, Protomyctophum crockeri* (Paxton, 1967, p. 429; Wisner, 1970, p. 426); and the melamphaid *Melamphaes lugubris* (Ebeling, 1962, p. 122).

Scopelarchus stephensi (fig. 58) is a central water mass species occurring in a narrow band, ca. 25.5°-34.5° N, across the northern portions of the Eastern and Western North Pacific Central Water Masses, from ca. 164° E to 126.5° W. S. stephensi apparently replaces S. michaelsarsi to the north of the Hawaiian Islands. Brinton's (1962, p. 72) chart of temperatures for the Pacific at 100 m. suggests that a shoaling of isotherms takes place at 25° N. This may indicate a thermal front at this latitude similar to that dividing the northern and southern Sargasso Sea at about 27° N in the North Atlantic (Backus, Craddock et al., 1969, pp. 87-106). Apparently associated with this thermal front is an eastward flowing subtropical countercurrent discussed by Yoshida and Kidokoro (1967, pp. 88-91), and Uda and Hasunuma (1969, pp. 201-210). I am hesitant to suggest that either feature is correlated with the southern boundary of Scopelarchus stephensi because this species is known from only 26 specimens taken in 12 hauls. More sampling needs to be done in order to confirm the intriguing distribution of this species. Ready examples of oceanic species with distributions similar to that of S. stephensi are not known to me, although the distribution of Sagitta pseudoserratodentata (Bieri, 1959, p. 11) or the distribution in the North Pacific of the euphausiid Nematoscelis atlantica (Brinton, 1962, p. 68) resemble that of S. stephensi, particularly the areas indicated as the main centers of abundance.

Benthalbella elongata (fig. 21) and B. macropinna (fig. 28) are both Antarctic species, no doubt circumglobal, concentrated mainly (on the basis of known captures) in the areas of maximum transport of the Antarctic Circumpolar Current (West Wind Drift) illustrated by Kort (1962, p. 4). These species occur from the Subtropical Convergence to well south of the Antarctic Convergence (the two convergences are defined and discussed by Sverdrup et al., 1942, p. 606). *Benthalbella elongata* is not known from north of the Subtropical Convergence, while only four specimens, two larvae, and two adults of *B. macropinna* are known from north of the Subtropical Convergence, all four in the Benguela Current region. The distribution of the known larval specimens of both of these species is somewhat to distinctly to the north of the records for the adults, and is no doubt associated with the shallower occurrence of larvae in waters with an equatorward component of motion. This is apparently typical for Antarctic species (McGinnis, pers. comm.).

Scopelarchoides kreffti (fig. 41), known from 10 specimens from five collections is apparently a member of the Subtropical Convergence Fauna discussed by Gibbs (1968).

The seven species exhibiting distributions crossing water mass boundaries show varying degrees of warm-water cosmopolitanism. These species are all central-tropical species using Ebeling's (1962, p. 129) terminology.

Scopelarchoides signifer is apparently limited to the Indian and Pacific Oceans (fig. 48), occurring in both Indian Equatorial and Central waters, throughout the island fringed seas of the western Pacific, and in a narrow band along the equator to ca. 138° W. S. signifer has also been taken in the Central South Pacific at 24.5° S, 155° W, near the Tubuai Archipelago. S. signifer apparently does not occur in the central North Pacific. The distribution of S. signifer is similar to that of Melamphaes danae and M. indicus, both central tropical species not occurring in the Atlantic, but the two melamphaids are known from the central North Pacific (Ebeling, 1962, pp. 123, 131). The Indo-Pacific distribution of Stomias affinis is nearly identical with that of S. signifer, but Stomias affinis occurs in the Atlantic (Gibbs, 1969, p. 15).

The distributions of *Scopelarchoides danae* and *Rosenblattichthys alatus* are quite similar to each other and except for the occurrence of *S. danae* in the Atlantic, quite similar to that of *S. signifer* (figs. 32, 41, 48). *S. danae* is known from only two isolated records in the Pacific. All three species apparently occur along the equator in the western and central Pacific but do not inhabit the eastern tropical Pacific.

Benthalbella infans is a nearly cosmopolitan warm-water species inhabiting the central and equatorial waters of all three oceans, but is not known from the eastern Pacific (fig. 24).

Scopelarchus guentheri is a circumglobal warm-water species occurring in all three oceans (fig. 55). In the Atlantic Ocean it occurs from nearly 15° N to 25° S, but apparently does not occur in North Atlantic Central Water. In the North Atlantic the distribution of this species falls within the Guinean. Amazonian, and Caribbean warmwater provinces proposed by Backus, Craddock et al. (1970), but is not known from the Gulf of Mexico. The record from the Caribbean is based on one (27.0) larva, which may have been carried there by the equatorial currents. The northern limit of S. guentheri in the Atlantic corresponds well with the boundary between North Atlantic Central Water and South Atlantic Central Water set by Backus, Mead et al. (1965) at 13.5-16° N, at 33 to 36° W, the boundary tilted from northeast to southwest, and detected by a deepening and divergence of the 15° C and 20° C isotherms. In the Indian Ocean S. guentheri is known from both Indian Equatorial and Central Water but adults are known only from Indian Equatorial Water. Of the seven species of scopelarchids known to occur in the Indian Ocean. only S. guentheri has been taken north of 5-10° N. This corresponds with the boundary found by Gibbs and Hurwitz (1967, p. 302) to delimit the distribution of Chauliodus pammelas from Chauliodus sloani (southern species), which they associated with a core of poorly oxygenated water occurring below the surface to the north of the boundary. The boundary was defined as the latitude at which the 1.0 ml/l dissolved oxygen isopleth occurs in the upper 200 m. As mentioned above, S. guentheri is one of the two known scopelarchids with noticeably elongate gill filaments, and perhaps its occurrence north of the boundary delimiting the distribution of other scopelarchids in the Indian Ocean can be explained in relationship to the dissolved oxygen content, but may also be an artifact of sampling effort.

In the far southern Pacific *S. guentheri* is known from the Subtropical Convergence and Transition region, where it occurs with the distinctive convergence fauna recorded by Gibbs (1968).

Scopelarchus guentheri is known from a band across the equator, from 170° E to 110° W, but is excluded from the main oxygen minimum areas of the eastern tropical Pacific. Although S. guentheri has been taken from Eastern and Western North Pacific Central Water and Eastern South Pacific Central Water, it is known from these areas only from larvae except for the nearshore waters around Hawaii as discussed below. S. guentheri occurs in the Transition Region off southern California.

In the Pacific Ocean central gyrals *S. guentheri* is known from the middle portions of these gyrals as follows: Central North Pacific, seven (18.0-43.6) specimens from five collections; Central South Pacific, three (23.6-43.4) specimens from three collections; nearshore waters

around Hawaii, five (23.6-102.5) specimens from five collections. This makes a total of 15 specimens from 13 collections of *S. guentheri* known from the middle portions of the central gyrals. From the Pacific Ocean as a whole, excluding the South China Sea and semi-isolated seas of the Indo-Malayan Archipelago, *S. guentheri* is known from 84 [48 (14.8-48.5) + 36 (50.0-119.0)] specimens from 61 collections. This, in connection with the evidence offered below, suggests that this species is more abundant around the periphery of the central gyrals and rare within the central portions of these gyrals.

The small dots on Figure 55 compare the distribution of *S. guentheri* (larger circles) with the combined distributions of *S. analis, S. michaelsarsi*, and *S. stephensi*. The latter three species are known from numerous hauls within the central portions of the gyrals with hauls to all depths between 0-1000 m. (the data is not sufficient to allow or disavow the possibility of vertical segregation of the species, but the larvae of all four occur above the thermocline in the surface layer). That these species are more abundant within the central portions of the gyrals is indicated by the fact that of the three, only *S. michaelsarsi* (fig. 58) is known from equatorial waters in the Pacific, and there only from the far western Pacific where the equatorial divergence is minimal (Reid, 1962).

On two Scripps Institution of Oceanography transects through the Philippine and South China Seas, S. analis was taken in the Philippine Sea, while S. guentheri was taken only in the South China Sea. In the transect at 34° S, 72°-92.5° W, reported by Craddock and Mead (1970), S. analis was captured only in the most offshore stations (two larvae from two collections) while S. guentheri (11 specimens from seven collections) was captured far inshore to the two records for S. analis except for one larval specimen. Numerous expeditions fishing the nearshore waters around Hawaii (King and Iverson, 1962; Clarke, pers. comm.) have revealed both S. guentheri and S. analis to occur in these waters, but whereas only five specimens of S. guentheri from five collections are represented in my material, S. analis is represented by 54 specimens from 25 collections (made to all depths between 0-1000 m). Finally, S. analis and S. michaelsarsi are well-known from North Atlantic Central Water, and many specimens of both have been taken in the western gyral area in the Sargasso Sea. S. guentheri is not known from North Atlantic Central Water.

In summary, 1 believe additional material will corroborate my hypothethis that *S. guentheri* is significantly more abundant around the periphery of the central gyral areas, and that it is rare within the middle portion of these gyrals, where it is replaced by *S. analis, S. michaelsarsi*, and *S. stephensi*. 1 believe that this must ultimately be related to food supply. I am in doubt concerning the applicability of this statement to the Indian and South Atlantic Oceans, but feel reasonably sure it represents the case in the Pacific. Distributions limited to or concentrated around the peripheries of the gyrals are known from other groups, e.g., *Euphausia recurva* and *Thysanopoda aequalis*, are apparently found in low concentrations in the middle portions of the gyral areas, where they are replaced by other euphausiid species in terms of abundance. These species are concentrated in more fertile, cooler waters of the subarctic boundary area, and equatorial Pacific (Brinton, 1962, pp. 207-208). The encirclement of *Melamphaes pumilus* by *M. simus* in the North Atlantic is probably another good example of this type of distribution (Ebeling, 1962, pp. 121-129).

Scopelarchus analis (fig. 52) is a circumglobal warm-water species known from all tropical water masses except Pacific Equatorial Water. This species does not occur south of the Subtropical Convergence. In all three oceans the distribution of *S. analis* corresponds well with the warm, saline central gyrals. *S. analis* occurs throughout the North and South Atlantic from 44° N in the eastern North Atlantic to 40° S. It is one of several scopelarchid species whose larvae have been taken due south, or nearly so, of the Cape of Good Hope, indicating that Africa does not completely isolate the Atlantic from Indian Ocean populations.

There are only 12 records constituting 17 specimens of this species from the Indian Ocean, most of them from the southern Indian Ocean, although *S. analis* is known from both Indian Ocean water masses.

In the Pacific this species occurs throughout the central water masses, both north and south, and its distribution extends to the Transition Region off southern California, but *S. analis* is apparently excluded from Pacific Equatorial Water.

A large number of oceanic species with distributions similar to that of *S. analis* can be found in the literature. A number of euphausiids, particularly *Euphausia brevis*, have Pacific distributions essentially identical to that of *S. analis* (Brinton, 1962, p. 207). McGowan (1971, p. 45) lists 10 oceanic species whose composite northern and southern end points in the North and South Pacific form a pattern essentially the same as the distribution of *S. analis*. Finally, *Melamphaes simus* and *M. danae* have Pacific distributions quite similar to that of *S. analis* (Ebeling, 1962, p. 131).

Scopelarchus michaelsarsi (fig. 58) is quite similar to S. analis in its distribution, but differs in three significant respects:

1. S. michaelsarsi does not occur in the eastern North Atlantic north of the equatorial region (fig. 58), whereas S. analis is well-known from

the eastern North Atlantic in the Canary Current off Europe and northern Africa. Both species occur in the western North Atlantic. In this respect the distribution of *S. michaelsarsi* is similar to that of *Diaphus luetkeni* (Nafpaktitis, 1968, p. 54) which occurs in the main subtropical gyral of the North Atlantic but does not occur in the eastern North Atlantic north of the equatorial region. The reasons for the exclusion of these two species (among others) from the eastern North Atlantic are unclear to me.

2. S. michaelsarsi is known from Pacific Equatorial Water, but only in the far west (170° E). A number of other Pacific Central species are known to cross the equator only in the western Pacific, e.g., Melamphaes danae (Ebeling, 1962, p. 131), Thysanopoda cristata and other euphausiids (Brinton 1962, p. 209), and a number of other oceanic species from various taxonomic groups listed by McGowan (1971, p. 45). S. analis does not enter Pacific Equatorial Water.

3. S. michaelsarsi is apparently replaced by S. stephensi north of Hawaii, as discussed above, but specimens of S. analis have been taken across the North Pacific, north to 40° N, and from off Japan to California.

One of the benefits derived from detailed systematic knowledge of a group is insight into the evolutionary history of the group that such knowledge provides. Understanding the history of a group may better enable us to understand the present day distribution of its extant species. Admittedly, the Scopelarchidae is probably an old group of fishes, no doubt extending back at least to the early Tertiary, although no fossil record is available. However, our increasing awareness of the importance of communities in the organization of oceanic faunas, and the strong hypothesis that species in communities have adapted to each other's presence through evolution, at least suggests that ecological factors controlling the present day distribution of species were important in the evolutionary history of those species. If so, the present day distribution of species should show some degree of concordance with the inferred history of those species. In any case, there are trends in the distribution of extant scopelarchid species that more or less correspond with my views of the evolutionary history of this group.

The most generalized scopelarchid species in terms of a number of characters are *Scopelarchoides signifer* and the species of *Rosenblattichthys. S. signifer* and *R. alatus* are central-tropical species, co-occurring over much of their ranges with five other scopelarchid species in the Indo-Pacific area. Both *S. signifer* and *S. danae* occur along the equator in the Pacific. *R. volucris* occurs in eastern Pacific Transitional Waters (at least in the north) and along the equator in the eastern Pacific. *R.*

hubbsi is known from only one specimen in the equatorial Atlantic. No specimens of *R. alatus* or *R. hubbsi* were available for osteological analysis, and the larvae of *R. hubbsi* are not positively known. I cannot with certainty describe the affinities of either species with *R. volucris* or with species of other scopelarchid genera. It seems likely that the origin of *R. volucris* may have occurred by separation of populations along the equator in the Pacific, with subsequent divergence. In similar fashion it seems likely that *Scopelarchoides nicholsi*, inhabiting Pacific Equatorial waters with a strongly developed core of poorly oxygenated water, may have arisen by separation of populations along the equator with subsequent divergence.

Aside from *Rosenblattichthys* and *Scopelarchoides nicholsi*, radiation in the Scopelarchidae appears to have been in two main directions—increasing adaptation to poorly productive central water masses and increasing utilization of high latitude areas. I believe there is evidence for two lineages within the family reflecting this radiation.

Scopelarchoides danae occurs in the Atlantic and may have originated there. S. signifer does not occur in the Atlantic. The probable close relationship of Scopelarchoides danae and Scopelarchus guentheri has been discussed above.

S. guentheri is a species probably most abundant around the peripheries of the central gyrals. S. analis, S. michaelsarsi, and S. stephensi are all abundant in the central portions of the central gyrals and S. stephensi is apparently limited to this habitat. The overall trend in this group of species appears to be radiation into the central gyrals from peripheral waters with perhaps a higher food supply. Trends in this group include reduction in body size, reduction in numbers of fin rays, lateral line scales and vertebrae, and an earlier onset of metamorphosis.

The other lineage of scopelarchids, that which led to the present species of *Benthalbella*, apparently represents a radiation from centraltropical waters into boreal and antarctic waters. *Scopelarchoides climax* is known only from the central South Pacific, *S. kreffti* only from the Subtropical Convergence area of the South Atlantic. *Benthalbella infans*, however, is a nearly circumglobal warm-water species. *B. linguidens* and *B. dentata* are limited to boreal and subarctic waters of the North Pacific, whereas *B. macropinna* and *B. elongata* are circumglobal in Antarctic Waters south of the Subtropical Convergence. Trends in this group of species include an increase in body size; an increase in numbers of fin rays, lateral line scales, and vertebrae; and a delayed onset of metamorphosis. Both sets of morphological trends, that of the lineage apparently radiating into central waters and that of the lineage radiating into polar waters, have been noted in other groups of fishes (e.g., Ebeling, 1962).

There have been few attempts, at least for midwater fish groups, to correlate phylogenetic inference with zoogeographic knowledge (among them Ebeling, 1962; Crane, 1966; Gibbs, 1969). My interpretation of the history of the Scopelarchidae agrees fairly well with Ebeling's (1962, p. 148) account of *Melamphaes*, and partially agrees with Gibbs' (1969, pp. 16-24) interpretation of the evolutionary history of the genus *Stomias*.

In summary, from a single, presumably central-tropical ancestor, the members of the family Scopelarchidae have radiated into virtually all geographic areas of the midwater habitat.

ADDITIONAL MATERIAL EXAMINED

I have examined much additional scopelarchid material since this report went to press. For most scopelarchid species represented by this additional material, the new records did not significantly enhance existing knowledge of distributional patterns, and these new records are not included in this report. For the five species listed below, part of the new material did add considerably to our knowledge of distributional patterns, and the appropriate distribution text figures have been altered to include this new information. The specimens listed below (by station number or by catalogue number) represent this important new material. My thanks to Dr. N. V. Parin for making available material from the Institute of Oceanology of the Academy of Sciences of the USSR (IOAN) and to Dr. C. R. Robins of the University of Miami for making available material from the Institute of Marine Science (UMML).

Benthalbella dentata. IOAN: R/V VITYAZ (V) 3153, V 3162, V 3248, V 4124, V 5605, V 6096.

Benthalbella infans. DANA: 3631 II. IOAN: V 4368, V 4680, V 4911, V 5139, V 6151; R/V PETR LEBEDEV 98.

Benthalbella linguidens. IOAN: V 2116, V 3151, V 3156, V 3162, V 3448, V 4052, V 5631.

Scopelarchoides danae. UMML: 19956, 19980, 19991, 20005, 20008, 20010, 22834, 22842, 22852, 22853, 22857, 22865, 22866, 22867, 22871, 22879, 23068, 24310, 24649, 26326, 26340, 26347, 27958, 28007.

Scopelarchus stephensi. IOAN: VITYAZ station at 26° 00' N, 164° 00' E.

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